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Biology of the Spotted Seatrout, Cynoscion nebulosus, in the Chesapeake Bay Region

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BIOLOGY OF THE SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*, IN THE CHESAPEAKE BAY REGION

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

by
Thomas F. Ihde
2000

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

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DEDICATION

This thesis is dedicated to my parents, Victor and Betty Ihde, who taught me to love nature, who encouraged me to dream, and who inspired me to follow my dreams.

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Last, but not least, I am eternally grateful to two very special people: my son Ian – whose fresh perspective always inspires me – and the love of my life, my best friend, my strength, my partner and my wife, Amy – I wouldn't have accomplished this without her.

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ABSTRACT

A comparison of aging structures has never been performed for the spotted seatrout anywhere in its range. To perform this comparison, 50 fish, ranging in size from 300 mm to 731 mm total length, were purchased August, 1997. The four most commonly used aging structures were compared by 1) processing efficiency 2) reader confidence 3) reader agreement (precision) 4) consistency of mark counts between structures and 5) growth with presumed age. Processing time was excessive for sectioned pectoral fin rays. Sectioned dorsal fin spines appeared clear and easy to read but mark counts were inconsistent with those of other structures and growth lacked a significant relationship with presumed age. Scale marks were often inconsistent, which led to low confidence and low agreement. Scale ages appeared to show systematic disagreement with otolith ages in a comparison plot. Sectioned otoliths were far superior to all other compared structures in all chosen criteria for aging spotted seatrout: marks were clearest, reader confidence was highest, agreement was 100% both within and between readers, and both fish size and structure size increased significantly with presumed age. Consequently, sectioned otoliths were found to be the preferred aging structure for spotted seatrout of the Chesapeake Bay region.

Validation – the process of determining the frequency of mark formation – has not been performed in spotted seatrout populations north of Florida. To validate the marks found on sectioned otoliths of this species, a size-stratified subsample (n = 683) was randomly selected from a total of 2766 spotted seatrout collected from June 1996 to March 1999 in the Chesapeake Bay region. Monthly marginal increment frequency plots and monthly frequency of 0 marginal increment plots showed that presumed annual mark formation occurred once a year during March and April, thus validating the sectioned otolith method in fish of ages 1 – 5 for the Chesapeake Bay region.

Spotted seatrout have long been recognized as a high quality food fish, and have been heavily exploited by both commercial and recreational fisheries. As such, this species must be carefully managed throughout its range. Life history information for populations north of Georgia has been sorely lacking, however, hence the objective of this study was to provide the age, growth, reproductive and mortality information needed for proper management of this northern population. A total of 2458 spotted seatrout were purchased from Chesapeake Bay commercial fishery catches June, 1996 to March, 1999. GSI values indicated a 5-month spawning season in the Chesapeake Bay. A single annual peak of spawning activity occurred the last week in May each study year. Females were first Fully Developed at 292 mm TL in the north, 40 – 60 mm longer than those of the south. However, maturity occurred at a similar age throughout the species' range. Chesapeake Bay spotted seatrout were longer at age than southern spotted seatrout. Female spotted seatrout were longer at age than males in the Chesapeake Bay, but males appear to survive longer. Von Bertalanffy growth parameters, and mortality estimates of this population were similar to those previously reported for southern populations.

Biology Of The Spotted Seatrout, *Cynoscion nebulosus,* In The Chesapeake Bay Region

General Introduction

The spotted seatrout, *Cynoscion nebulosus* (Cuvier), is an estuarine species of the family Sciaenidae. Typically one of the top consumers in an estuary (Tabb, 1958), spotted seatrout are predators throughout their lives. Fish less than 45 mm feed mainly on copepods (McMichael and Peters 1989), but once greater than 15 mm, they supplement copepods with mysids and eventually with small shrimp and fish. Young fish continue to feed mainly on shrimp until they reach about 150 mm, when they begin to consume a greater portion of fish and larger crustaceans in their diet (Moody, 1950; Overstreet, 1983; McMichael and Peters, 1989).

Though this species ranges along the Atlantic and Gulf of Mexico coasts from New York to Campeche, Mexico (Welsh and Breder, 1923; L. Sánchez-Velasco et al., 1996), it exists as separate subpopulations in individual estuaries, as indicated by tagging studies (Moffett, 1961; Iversen and Tabb, 1962; Overstreet, 1983; Baker et al., 1986), electrophoretic comparisons (Weinstein and Yerger, 1976), and mitochondrial DNA diversity (Gold et al., 1999).

Spotted seatrout prefer shallow areas of the estuary (Mahood, 1975; Lorio and Perret, 1978) and are associated with a variety of substrates, including submerged vegetation, sand, shell reefs and other structures (Moody, 1950; Tabb, 1958; Mahood, 1975; Lorio and Perret, 1978). Moody (1950) suggested that seatrout habitat preference likely depends on food availability.

The spotted seatrout is an extremely euryhaline species that tolerates salinities from 0.2 ppt (Perret, 1971) to 75 ppt (Simmons, 1957) and a wide range of temperatures from 5 - 30°C (Lorio and Perret, 1978). This species is reported to respond to temperature extremes by moving from shallow to deep areas of the estuary or offshore, where temperature is more stable (Welsh and Breder, 1923; Pearson, 1929; Tabb, 1958; Mahood, 1975). Brown (1981) and Hildebrand and Schroeder (1928) assumed an annual southern migration of spotted seatrout to escape the winter temperatures of the Chesapeake Bay. Chesapeake Bay spotted seatrout likely winter south of Cape Hatteras where water temperatures remain higher in the winter (J. Musick, 1999; personal communication). This relatively short migration (about 200 km) is easily within the known migration patterns of well-studied populations (Moffett, 1961; Iversen and Tabb, 1962; Overstreet, 1983; Baker et al., 1986), and is probably undergone by the majority of the Chesapeake Bay population. However, some adult spotted seatrout are caught in the Bay year round, and many fish appear to stay there in relatively warm winters.

Welsh and Breder (1923) caught spotted seatrout in Chesapeake Bay in December, and Massman (*In* Tabb, 1958) reported that spotted seatrout were resident in the Bay all winter. The number of resident winter spotted seatrout is likely dependant on temperature, as I collected many fish in the Chesapeake Bay over the exceptionally warm winter of 1998-1999, when mean daily water temperatures at the Bay mouth never dropped below 5.2°C [Center for Operational Oceanographic Products and Services (CO-OPS) division of

NOAA/NOS 1999, personal communication]. During that winter, fish were collected in the Bay in November, December, February and March. Even in January, the gill net fishery caught fish just outside the Bay mouth near Rudee Inlet (see Fig. 1 in Chapter 1). The lack of many fish from the Chesapeake Bay in previous studies in warm-winters may reflect a lack of fishing effort since many Chesapeake Bay haul-seine fishermen shift their efforts to the oyster and striped bass fisheries during these months and don't fish at all in January (J. Owens, VIMS Fisheries, 1999; personal communication). Vetter's 1982 study indicated that spotted seatrout can metabolically compensate for temperature extremes if the shift is gradual; however, it should be noted that fish in his study were never exposed to temperatures less than 15°C. Winter fish kills, which have often been reported for spotted seatrout (Pearson, 1929; Gunter, 1941; Gunter and Hildebrand, 1951; Tabb, 1958), likely reflect temperature drops too rapid for metabolic compensation (Gunter and Hildebrand, 1951; Massman *In* Tabb, 1958; Vetter, 1982).

Spotted seatrout have long been recognized as a fine-quality food fish (Lawson, 1709 *in* Smith, 1907; Goode, 1884; Pearson, 1931; Hildebrand and Cable, 1934; Tabb, 1966), and they are highly sought after by both commercial and recreational fisheries (Pearson, 1931; Merriner, 1978). Such a highly prized species needs to be carefully managed throughout its range. To date, however, very little work has been done on this species north of Georgia.

Brown's (1981) work in the Chesapeake Bay is the only study on the northern populations of spotted seatrout to date. Brown's age and growth work, however, was based solely on unvalidated scale-aging. Since her work, unfortunately, the scale method has been seriously questioned for fishes in general (Beamish and McFarlane, 1983). In addition, no comparison of aging structures has been performed anywhere in the range of the spotted seatrout, even though many workers consider this initial procedure essential to sound age and growth study (Williams and Bedford, 1974; Chilton and Beamish, 1982; Casselman, 1983). And validation, an assessment of accuracy in aging methods, has not been performed on any aging structure for spotted seatrout north of Florida, though validation is also considered essential for sound age and growth study (Beamish and McFarlane, 1983).

Accordingly, this thesis:

1) compares calcified structures for aging spotted seatrout of the Chesapeake Bay;
2) validates marks on sectioned otolith from this species; and
3) describes age composition, growth, spawning periodicity, age at maturity and mortality estimates.

Chapter 1

Comparison of calcified structures for aging spotted seatrout in the Chesapeake Bay region

Introduction

There have been many studies on the age and growth of spotted seatrout, especially on southern populations. Most of these studies relied on scale-based aging (Pearson, 1929; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Tabb, 1961; Iversen and Tabb, 1962; Brown, 1981; Wade, 1981; Rutherford, 1982; Colura et al., 1984; Wakeman and Ramsey, 1985), but a few employed sectioned otolith techniques (Sundararaj and Suttkus, 1962; Maceina et al., 1987; Murphy and Taylor, 1994). Though ages up to 15+ years (scale age) have been reported for this species (Brown, 1981), the accuracy of these age estimates has not been assessed beyond age 3 for scales or age 5 for otoliths, and accuracy has not been assessed for any aging technique in populations north of Florida.

Since the usefulness of calcified structures for aging can vary geographically, many workers have suggested that several structures should be evaluated for both accuracy and precision in each population studied (Chilton and Beamish, 1982; Beamish and McFarlane, 1983; Casselman, 1983). No such comparison has ever been published for spotted seatrout anywhere in their range, however, and no structures other than scales or otoliths have been used in aging.

The primary objective of this study was to determine the best calcified structure for aging spotted seatrout of the Chesapeake Bay region by comparing the four structures most commonly used for aging fish (Chilton and Beamish, 1982; Brothers, 1983): otoliths, scales, fin spines, and fin rays. Criteria to determine the “best” aging structure included: 1) processing efficiency, 2) reader confidence, 3) reader agreement (precision) – both within and between reader(s), 4) consistency of mark counts between structures, and 5) growth of both the structure and the fish with presumed age. A secondary objective was to evaluate the usefulness of whole otoliths for aging spotted seatrout, because whole otoliths could be a timesaving alternative to sectioning if they proved useful.

Methods

Collection of fish

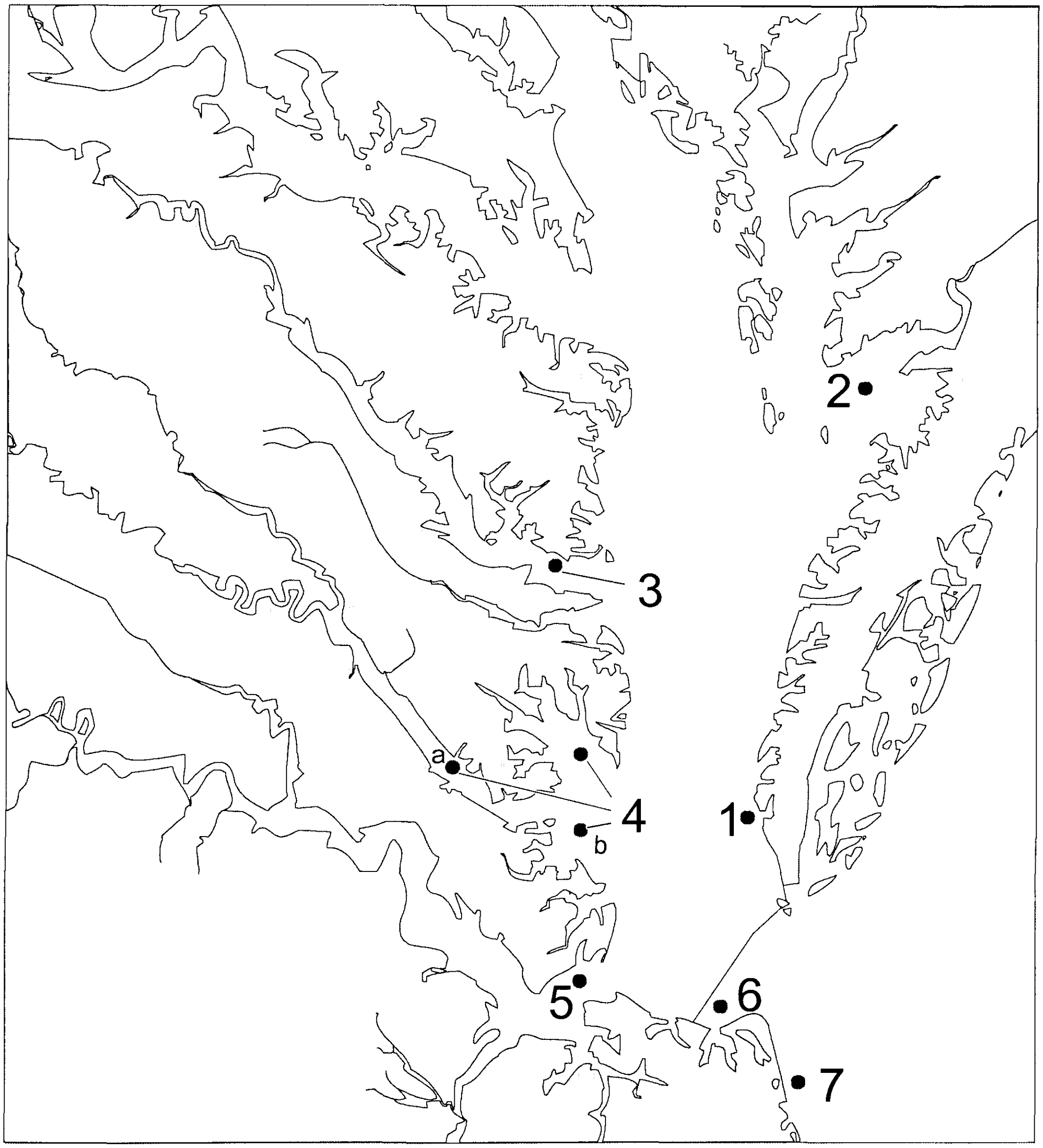
Collection for this study was limited to one month – August 1997 – to minimize mark variation within each calcified structure, and to avoid difficulties in interpreting the edge of a structure during the period of annulus formation. August was chosen because this month is far from the time of annulus formation (Moffett, 1961; Tabb, 1961; Maceina et al., 1987) and because a wide size range of fish was readily available from the Chesapeake Bay then. All fish were caught in commercial haul-seines in either Lynnhaven Inlet or Mobjack Bay (Fig. 1).

To include as many age groups as possible, 20 fish from each of three length strata were sought from the catch: 1) small fish – under 380 mm total length (TL), 2) medium fish – 380 to 509 mm and 3) large fish – over 510 mm. Only 10 large fish were successfully collected, however. The fish collected ranged in size from 300 mm to 731 mm.

Standard length (SL), total length (TL), girth (G), total weight (TW), eviscerated weight (EW) and sex were recorded on each of the 50 fish collected. Torn or damaged caudal fins were common; consequently, calculations are based on SL. Unless otherwise noted, reported TL values are based on the SL – TL relationship observed in 1357 fish:

$$TL = 10.56 + 1.1537 * SL \qquad (100\ r^2 = 99.5\%)$$

Figure 1. Collection locations for spotted seatrout.



1 - (Southern) Eastern Shore
2 - Pocomoke Sound
3 - Rappahannock River
4 - Mobjack Bay
  - a) York River
  - b) Poquoson Flats
5 - James River
6 - Lynnhaven Roads
7 - Rudee Inlet

The first spinous dorsal fin, and the left soft-rayed pectoral fin were removed from each fish, placed flat in kraft (coin) envelopes and stored frozen, following Chilton and Beamish (1982). Both sagittal otoliths were removed, wiped clean, and stored dry as pairs in plastic cell wells typically used in cell culture work. Scales were removed from a location just above the lateral line, between the first and second dorsal fin, and stored dry in kraft envelopes. This location was chosen because preliminary study showed scales from below the lateral line and behind the pectoral fin, the standard location for spiny-rayed fishes (Lagler, 1952), were mostly regenerated and of little use.

Preparation of calcified structures

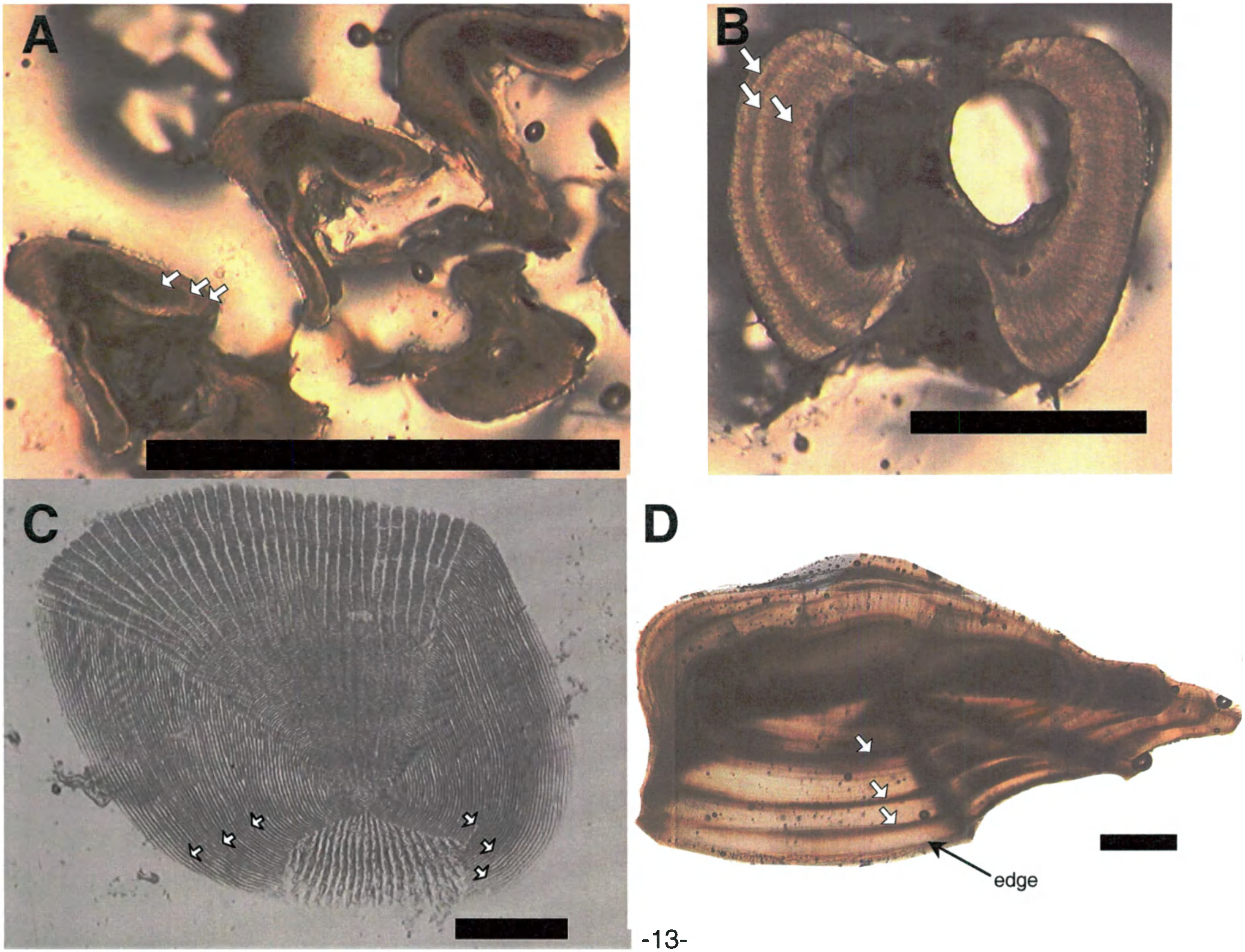
Specific pectoral fin rays and first dorsal fin spines were chosen for analysis based on a preliminary review of all possible rays and spines of the sectioned fins of two fish, one 463 mm and the other 643 mm TL. Preliminary review indicated that rays and spines of intermediate size were most desirable. Pectoral rays no. 6 - 8 possessed small vascular cores, the most distinct presumed annular marks and the greatest number of observed marks compared to all other rays. Similarly, dorsal fin spine no. 2 was taken because it possessed a small vascularized core, distinct marks, and the maximum number of observed marks compared to the other dorsal fin spines.

Progressive 0.5 mm sections were taken in the preliminary review to determine the optimal location for sectioning the rays and spines. Optimal sectioning distances appeared to be 3 and 4 mm from the base of the rays and spines, respectively, so only these distances were used when sectioning subsequent pectoral fin rays and dorsal fin spines.

Fin rays and spines were prepared for reading by first dipping whole fin structures in boiling water for about one minute. Then excess tissue was wiped away, and the structures were air-dried. Dried structures were mounted on cardboard for cross-sectioning following Chilton and Beamish (1982), but I used Crystalbond™ (Aremco Products, Inc.) adhesive rather than epoxy for mounting. Cross-sections were then taken from the initial mounts, mounted again (not immersed) in Crystalbond™ on glass slides, and viewed in transmitted light under a microscope to enumerate presumed annular marks. Annular marks (see Fig. 2A, 2B) were presumed to be the distal edge of the translucent bands (Williams and Bedford, 1974; Chilton and Beamish, 1982; Casselman, 1983). When a mark appeared at the edge of the structure, it sometimes was difficult to determine if it was an actual mark or merely an artifact of preparation. Viewing the structure in reflected light was helpful in these cases, since presumed marks then appeared as dark bands.

Scales were cleaned before mounting by immersing them in warm water and gently brushing them as required. Scales were then taped to acetate sheets (0.02 gauge) and pressed between two additional acetate sheets in a Carver® Laboratory Press (Model-C equipped with heated platens) for 2 min at 20,000 psi and 75 °C. Scale impressions were then viewed at 20x and 32x on a Bell-Howell R735 microfiche reader to enumerate presumed annular marks. Presumed annular marks on the ctenoid scales (see Fig. 2C) of the spotted seatrout were determined primarily by "cutting over" (Lagler, 1952) where a completed circulus or ridge forms past the unfinished endpoint(s) of one or more incomplete circuli in *both* lateral fields of the scale. The presumptive annual mark on scales was

Figure 2. Comparative appearance of presumed annual marks on sectioned pectoral fin rays (A), a sectioned dorsal fin spine (B), a scale (C), and sectioned otolith (D) of three spotted seatrout. Structures A and D are from the same fish. The pectoral fin ray sections show rays no. 6 (upper right) - 8 (lower left). The dorsal fin spine shows a section of spine no. 2. The closed arrow in D indicates the edge of the otolith section. Presumed annual marks are indicated by arrows. All images were taken in transmitted light. The solid bar marks are 1 mm in length.


A
B
C
D
edge

generally accompanied by: 1) the origin of multiple secondary radii; 2) a clear, narrow zone in the anterior field; and 3) an additional ridge in the posterior field of the scale in presumably older fish.

Either the right or left otolith was chosen randomly for transverse sectioning. If necessary, the chosen otolith was first brushed clean with a dilute bleach solution and thoroughly rinsed. The nucleus was marked for sectioning, sulcal side down, on a lighted slide viewer. Marked otoliths were then mounted, sulcal side down, onto cardboard for sectioning as described for fin rays and spines. Progressive sections were made until a clear view of the “true center” (Williams and Bedford, 1974) of the nucleus was obtained, where the angular walls of the sulcal groove were observed to meet at a point (Chilton and Beamish, 1982). Sections were then immersed in Crystalbond™ on a glass slide for viewing and enumeration of presumed annular marks. Annular marks were presumed to be the distal edge of the translucent bands (Fig. 2D) (Williams and Bedford, 1974; Chilton and Beamish, 1982; Casselman, 1983).

Immersion of the otolith sections in Crystalbond™ reduced light refraction off the surface of the section and allowed for easier viewing of the presumed mark(s). This medium offered several advantages over a liquid cover slip (e.g. Flo-texx, described by Chilton and Beamish, 1982): 1) there was no need to treat sections with oil prior to immersion to improve clarity of growth zones, 2) Crystalbond™ fully hardened immediately upon cooling, and 3) sections were easily repositioned or even removed from the medium if desired after initial mounting. The only disadvantage to Crystalbond™ was the presence of bubbles sometimes found in the medium, and the production of bubbles with excessive heating.

All structure sections were made with a variable-speed Buehler Isomet jeweler's saw, and sections were viewed on a Wild stereomicroscope at magnifications of 120 - 1000x, or on a Zeiss compound microscope at magnifications of 1000x or greater.

Evaluation of aging structures

Processing efficiency was evaluated by comparing mean time required for processing and reading each structure, per fish (Gaichas, 1997). Reader confidence was evaluated by having each reader assign a confidence to each structure read; a ranking of 1 (low confidence) to 5 (high confidence) was based on the clarity of the presumed annular mark(s), as recommended by Casselman (1983). Differences in confidence rankings between structures were tested with the Mann-Whitney test for ordinal data (Minitab®,1996; Zar, 1996).

Within reader agreement was evaluated by percent age agreement between the first and second readings by one reader; and between reader agreement was evaluated using percent agreement between the first readings by two readers. All readings were done independently and without knowledge of fish size. Second readings were done using a randomized order of sections with at least a week between readings.

Consistency of mark counts between structures of the same fish, a verification procedure described in Brothers (1983), was evaluated using a linear regression t-test to reveal if two aging structures showed significantly different counts. The null hypothesis in this t-test was that the slope of the regression line equaled 1, i.e. x equals y, so that there was no difference in counts between the two aging structures. The coefficient of determination, 100 r^2 (Zar, 1996) was used to quantify the amount of variation in "y" [a) scales, b) spines and c) spines in Table 1] that was associated with variation in "x" [a) otoliths, b) otoliths and c) scales in Table 1]. Consistency of mark counts between structures was also examined using a test of symmetry following Hoenig et al. (1995). The null hypothesis for the test of symmetry was that there was no systematic difference in counts between the two aging structures. It is notable that both of these tests -- the t-test and the test of symmetry -- can only indicate a significant difference in age counts between two structures and cannot indicate which structure is better to use. The tendency of a structure to overage or underage a fish was based on the assumption that otoliths age counts are the most accurate. This assumption was based on: 1) Casselman (1983), who states that otolith readings are generally more reliable than other structures, 2) Bagenal (1974) who points out that otoliths are not thought to be subject to resorption like other calcified structures, and 3) Lowerre-Barbieri et al. (1993) who found otolith readings to be highly precise and accurate for ages 1 – 5 for the closely related weakfish (*Cynoscion regalis*) in the Chesapeake Bay region. This assumption was later confirmed for Chesapeake Bay spotted seatrout by validation (see Chapter 2).

Growth with presumed age was evaluated in two ways. First, linear regression (SAS, 1991; Zar, 1996) of the standard length of the fish on presumptive age (mark counts) was used to determine if fish size increased with presumed age, as would be expected if an aging technique were useful.

Second, linear regression of the calcified structure size on presumptive age was used to determine if structure size increased with presumed age.

To express structure size, sectional surface area, excluding vascularized core area(s), was used as a measure of fin ray and spine growth, and scale radius and whole otolith length were used as measures of scale and otolith size, respectively. Calibrated measurements of fin ray and spine surface areas and scale radii were taken with a compound video microscope and the Optimas® (version 6.0) image analysis system. In doing so, scale radius was measured from the focus to the scale edge at the (ventral) angle where circuli curve from the anterior field to the lateral field. And finally, whole otolith length was measured from the tip of the rostrum to the mid-posterior edge using an ocular micrometer at 120x.

Comparison of whole and sectioned otoliths

To evaluate whole otoliths in comparison to sectioned ones, a separate, larger, size-stratified subsample (n = 782) was selected from all fish collected from 1996 - 1999. Processing methods for this comparison follow those described above for sectioned otoliths, except that the whole otolith was aged by enumerating presumed annual marks before sectioning. In doing so, the presumed annual mark was taken as the proximal edge of the opaque growth bands observed in transmitted light on a lighted slide viewer. Confidence rankings were assigned to each whole otolith reading, as described above. The whole otolith – sectioned otolith readings were then compared using: 1) a comparison of reader confidence using a Mann-Whitney test for ordinal data (n = 576 fish) as described above, and 2), a comparison of the consistency of mark counts between structures of the same fish (n = 782) using both a linear regression t-test and a test of symmetry as described above.

Results

Comparative appearance of aging structures

Sectioned pectoral fin rays were comparatively small structures (Fig. 2A), with marks that were often difficult to read and interpret. These marks seemed to indicate age, but early marks were sometimes obscured or consumed by the vascular core of the fin ray. Further, marks were only visible under high magnification, and even then they were faint and difficult to read.

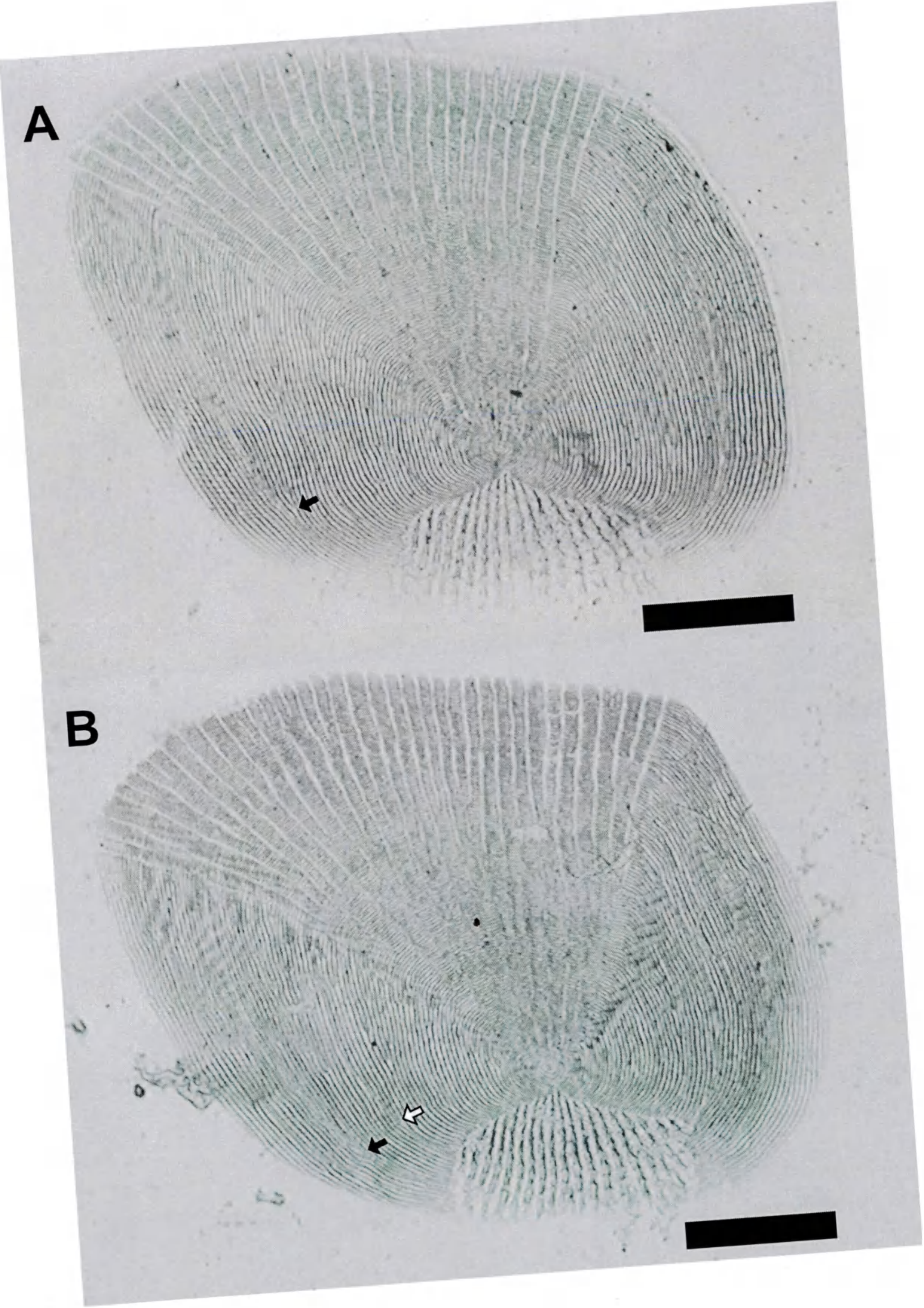
Sectioned dorsal fin spines were relatively large structures that showed initially promising, clear, well-defined marks (Fig. 2B). Dorsal fin spines however, like pectoral fin rays, have vascular cores that may eventually consume early marks.

Scales showed presumed annual marks that were often clear and well defined (Fig. 2C). However, various inconsistencies often made scales difficult to read and interpret. For example, in one type of inconsistency, scale marks – indicated by some degree of “cutting over” – were present in only one lateral field of an individual scale with no indication of a mark in the same position of the opposite lateral field (Fig. 3). In a second type of inconsistency, a mark was very distinct on one scale but not evident on a neighboring scale of the same fish (Fig. 4).

Sectioned otoliths were large structures. Their presumed annular marks were consistently clear, well defined (Fig. 2D) and consequently easy to read.

Figure 3. An illustration of inconsistency between the number of marks in each lateral field of a spotted seatrout scale. Solid arrows indicate presumed annual marks. Note the additional mark or "check" (indicated by the open arrow) present in the left lateral field but absent in the right lateral field.

Figure 4. Inconsistency observed in marks between two scales from the same fish, a 376 mm TL female fish. The solid arrows indicate presumed annual marks. The open arrow (in scale B) indicates an additional mark or “check” not visible in scale A. This fish was aged “1+” by both scales and sectioned otoliths.


A
B

Evaluation of structures using chosen criteria

Processing time was excessive for sectioned pectoral fin rays. The mean time required to prepare and read pectoral fin rays (75.2 min per fish) was nearly five times greater than that required for dorsal fin spines, the most time-consuming of the other three structures (Fig. 5). Consequently, pectoral fin rays were excluded from all further analysis. Mean processing times were reasonable for all the other structures, although sectioned dorsal fin spines (at 15.4 min/fish) required two – three times as much processing time as either sectioned otoliths (6.5) or scales (8.1).

Reader confidence was greatest for sectioned otoliths. The confidence ranking of 4.90 ± 0.03 standard error (SE) for sectioned otoliths (Fig. 6) was significantly greater than that of scales (3.35 ± 0.16 SE) or dorsal fin spines (3.50 ± 0.18 SE). There was no significant difference between confidence rankings of scales or dorsal fin spines.

Agreement between readings was greatest by far for sectioned otoliths. Within reader agreement was 100% between the first and second otolith readings of reader 1 and reader agreement was 100% between the first readings of reader 1 and reader 2. In comparison, scale agreement was 94% within readers, but only 74% between, while dorsal fin spine agreement was only 86% within readers and 74% between.

Presumed age counts using dorsal fin spines were generally not consistent with counts using either sectioned otoliths or scales. Dorsal spines showed only 10% agreement with ages determined using sectioned otoliths and only 36% agreement with scales (Table 1). Linear regression t-tests rejected the

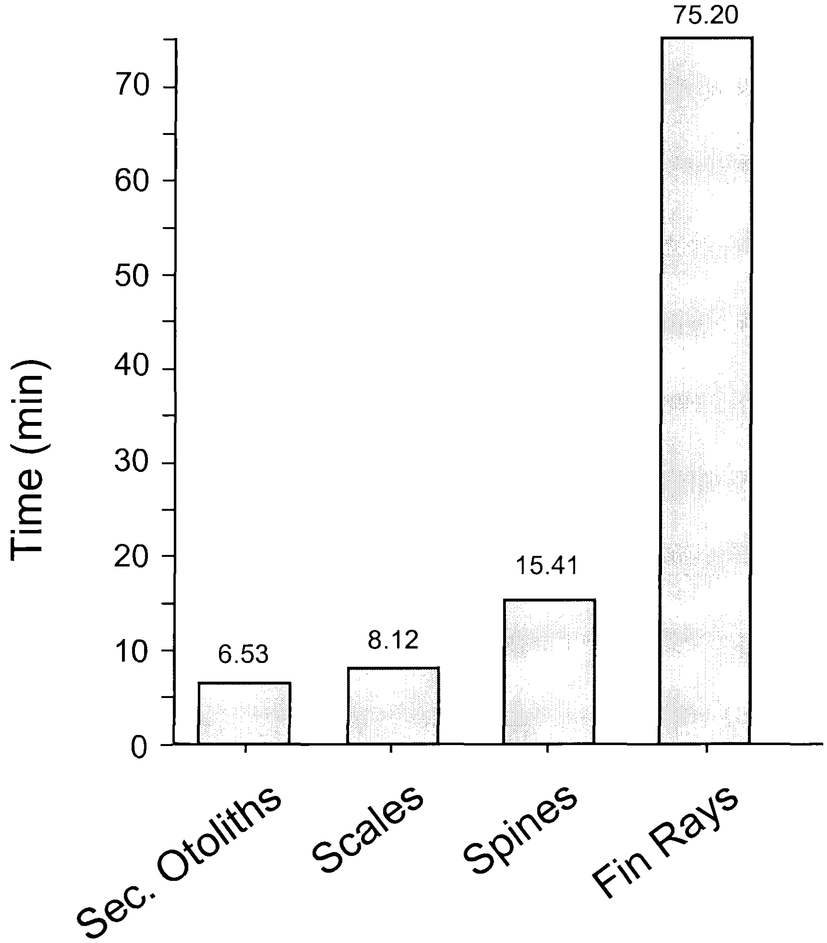


Figure 5. Efficiency of processing expressed as the time required to prepare and read sectioned otoliths, scales, dorsal fin spines and pectoral fin rays of spotted seatrout. Numbers above each bar are mean processing time.

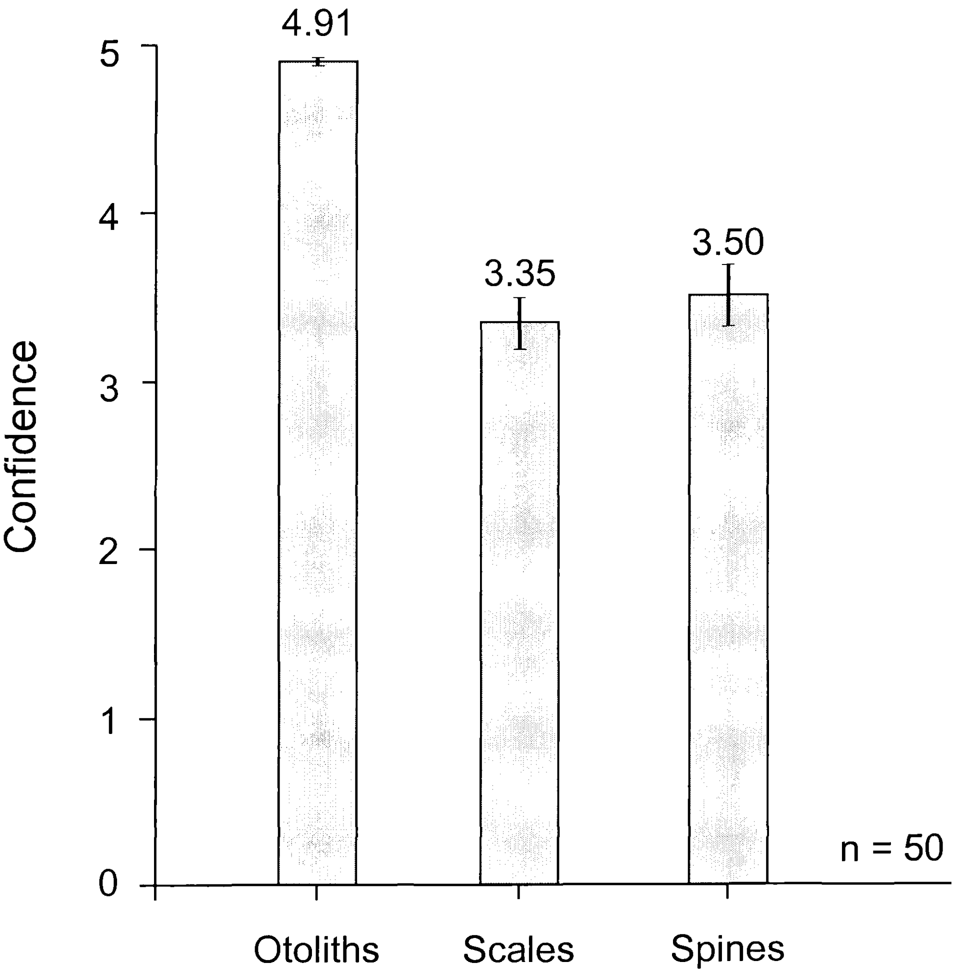


Figure 6. Reader confidence in sectioned otolith, scale and dorsal fin spine age readings for spotted seatrout. Error bars are ± standard error (SE).

	Structures Compared	% Agree	100 r^2	t Value	Test of Symmetry (P)
a.	**Scales with Otoliths**	86%	90%	-6.99	$0.05 < P < 0.10$
b.	**Spines with Otoliths**	10%	6%	-9.28	$P < 0.001$
c.	**Spines with Scales**	36%	6%	-6.95	$P < 0.001$

Table 1. Summary of test statistics comparing presumed age counts for (n = 50) individual spotted seatrout scales, sectioned otoliths, and dorsal fin spines. The t values given evaluate the null hypothesis that the slope equals 1, where the critical value for $t_{0.05(2)\ 48df}$ is 2.011. The test of symmetry expresses the probability (P) that the null hypothesis of 1:1 count correspondence is true.

null hypotheses that $\beta = 1$, implying significant differences ($P < 0.0001$) in presumed age counts between dorsal fin spines and otoliths and between dorsal spines and scales. Dorsal fin spines generally overaged age 1 and age 2 fish and underaged fish greater than age 2 when compared with presumably correct ages from sectioned otoliths (Fig. 7a). Some fish aged as 1 using sectioned otoliths were aged as 3 or 4 using dorsal fin spines, and one fish aged as 5 using otolith age was aged as only 3 using dorsal spine age. Only 6% of the variation in dorsal spine age was associated with the variation in either otolith or scale age. And finally, a test of symmetry rejected the null hypothesis that dorsal spine ages do not show systematic differences from otolith ages ($P < 0.001$) or from scale ages ($P < 0.001$).

Presumed age counts using scales showed generally high agreement with counts using sectioned otoliths, but there also appears to be systematic disagreement between these structures. Scale age showed 86% agreement with ages determined using sectioned otoliths (Table 1). The linear regression t-test, however, rejected the null hypothesis that $\beta = 1$, implying significant differences ($P < 0.0001$) in presumed age count between scales and sectioned otoliths. Scales generally overaged age 1 fish and underaged fish greater than age 2 when compared with presumably correct sectioned otolith ages (Fig. 7b), however, age differences between scales and otoliths were limited to 1 year for the otolith age range of 1 to 5 represented here. 90% of the variation in scale age was associated with the variation in sectioned otolith age, and a test of symmetry failed to reject the null hypothesis that scales do not show systematic difference from sectioned otolith ages (Table 1).

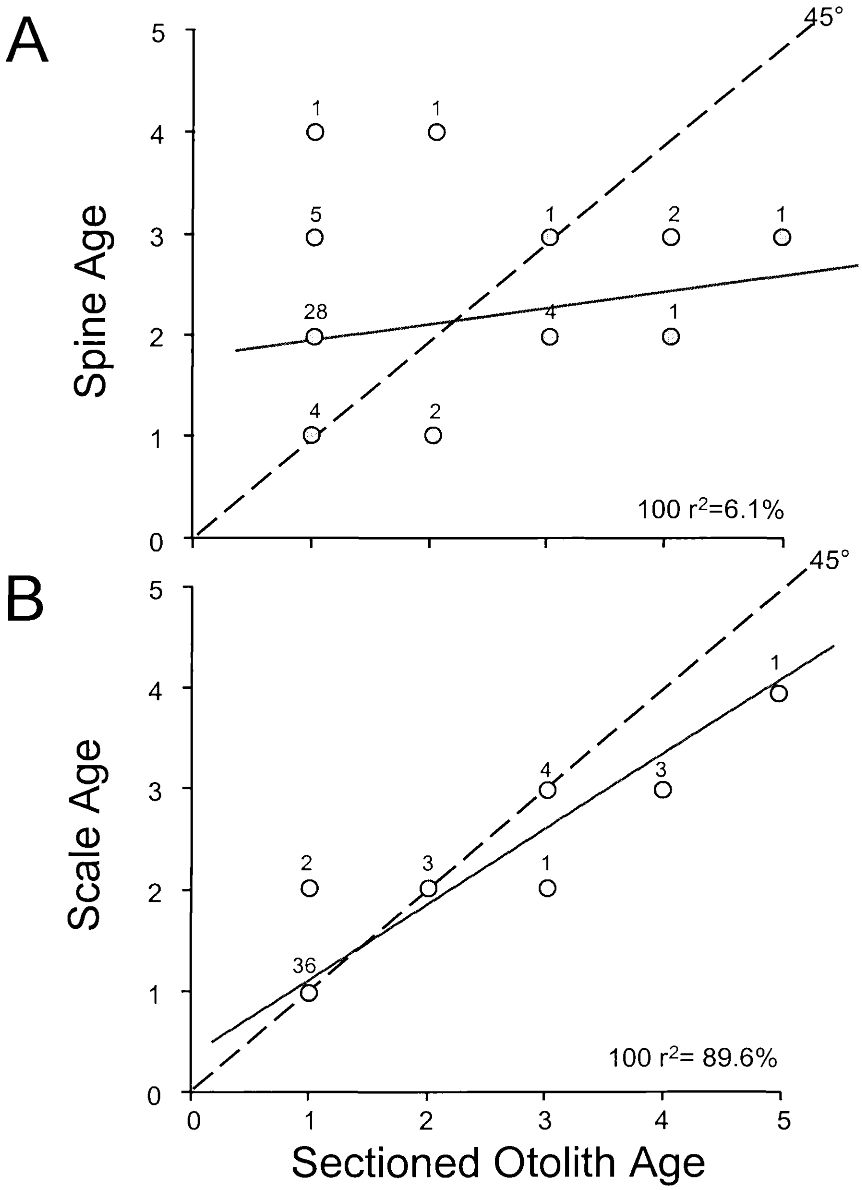


Figure 7. Regression of spine age (A) and scale age (B) on sectioned otolith age to evaluate agreement between aging structures. The dashed 45° diagonal represents 1:1 correspondence of age readings. Numbers represent the frequency of observations at each point.

Fish size increased significantly with presumed age ($P < 0.0001$) for both sectioned otolith and scale ages; however, no significant relationship was found for sectioned dorsal fin spines ($P < 0.1628$) (Fig. 8). The size of the aging structure also increased significantly with presumed age for both sectioned otolith and scale ages ($P < 0.0001$), but again, no significant relationship was found for sectioned dorsal fin spines ($P < 0.2695$) (Fig. 9).

Comparison of whole and sectioned otoliths

Sectioned otoliths were generally superior to whole otoliths. Although agreement was high between whole and sectioned otoliths (87%) and though 91% of the variation (100 r^2) in whole otolith age was associated with the variation in sectioned otolith age, reader confidence was significantly greater for sectioned otolith counts. Mean confidence values were 4.97 ± 0.0079 SE for sectioned otoliths but only 3.29 ± 0.043 SE for whole otoliths (Fig. 10). Linear regression t-test rejected the null hypothesis that $\beta = 1$, implying significant differences in ages between whole and sectioned readings of the same otolith ($P < 0.0001$). Finally, a test of symmetry also rejected the null hypothesis that there was no systematic difference between sectioned and whole otolith ages ($P < 0.001$). Since surface features on whole structures can be misleading, it was assumed that sectioned otoliths (validated in Chapter 2) resulted in more accurate aging than whole otoliths, as such, whole otolith ages tended to overage fish at ages less than 3 and to underage fish at ages greater than 3 in comparison to sectioned otolith ages (Fig. 11).

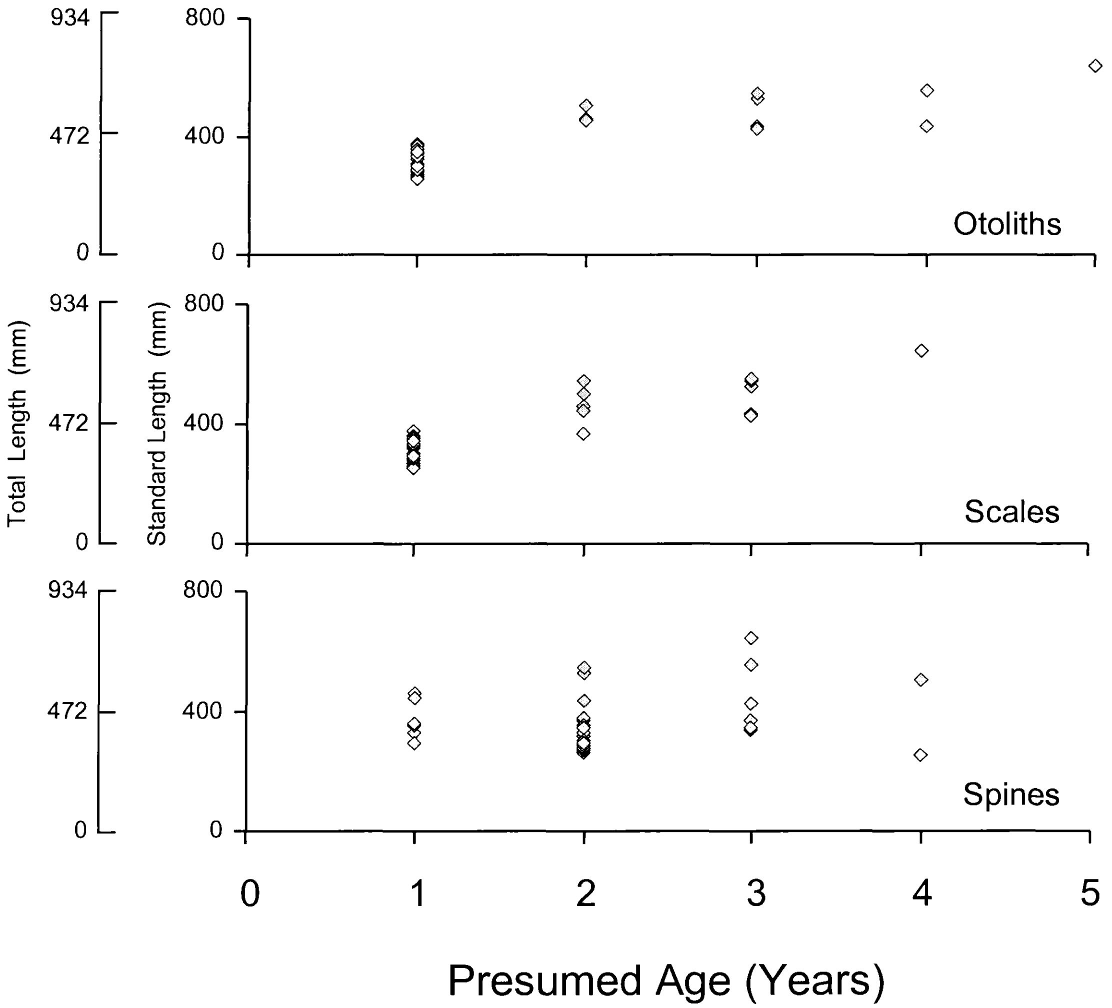


Figure 8. Lengths of spotted seatrout in relation to presumed ages of sectioned otoliths, scales and dorsal fin spines.

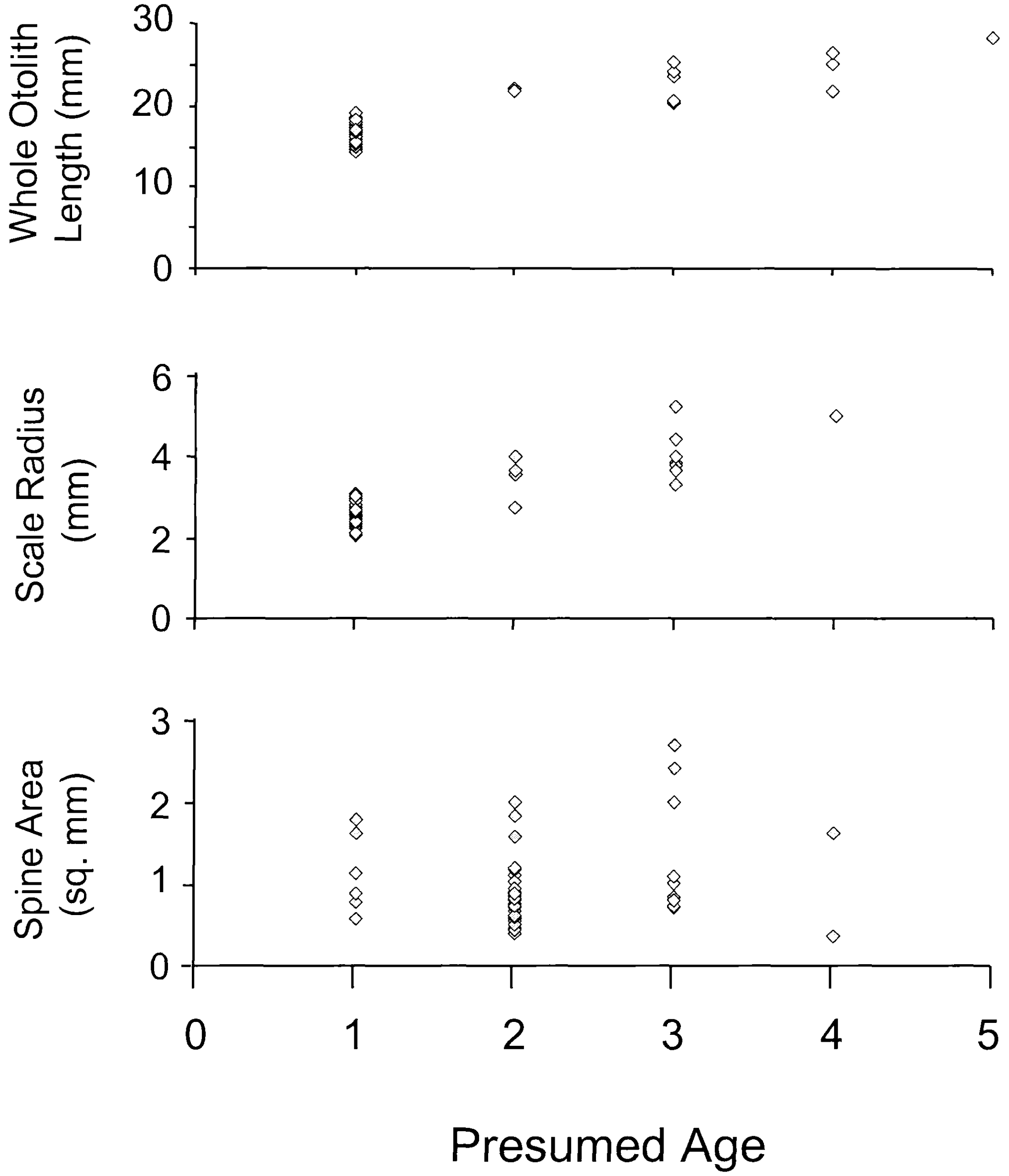


Figure 9. Structure size in relation to presumed age for otoliths, scales and sectioned dorsal fin spines of spotted seatrout. Otolith size was measured on whole otoliths, but presumed ages were read from sectioned otoliths.

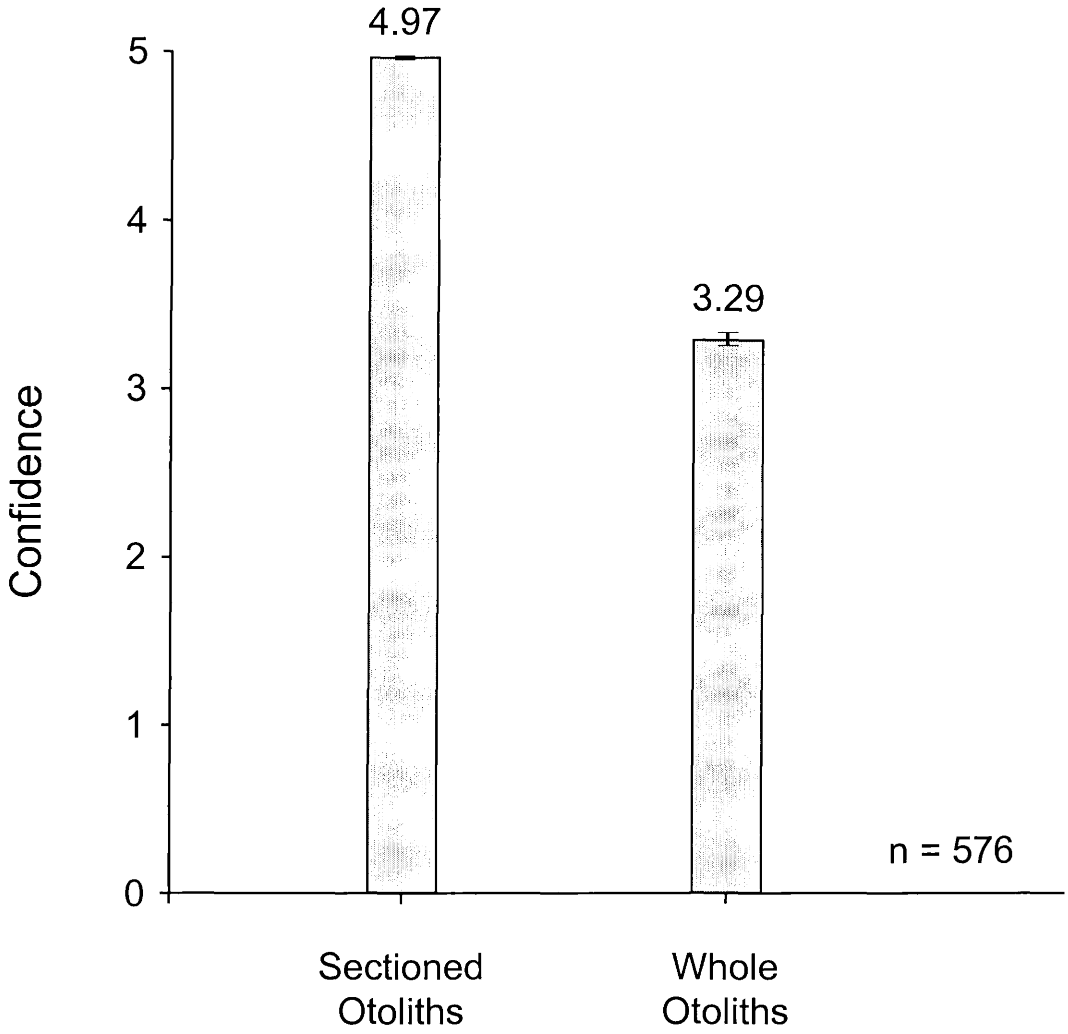


Figure 10. Reader confidence for sectioned and whole otolith age readings in Chesapeake Bay spotted seatrout. Error bars are ± standard error (SE).

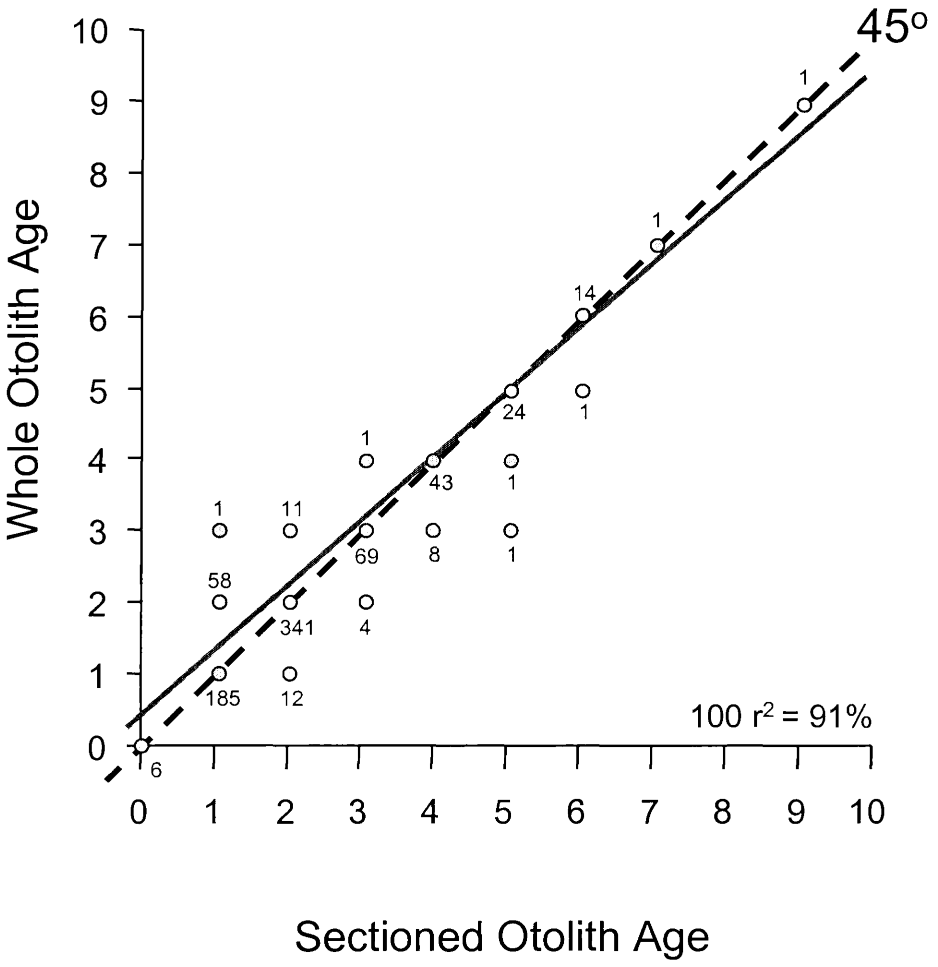


Figure 11. Regression of whole otolith age with sectioned otolith age to evaluate agreement between structures. The dashed 45° diagonal represents 1:1 correspondence of age readings. Numbers represent the frequency of observations at each point.

Discussion

Sectioned pectoral fin rays were found to be unreasonable as an aging structure early in this study, and though sectioned dorsal fin spines showed initial promise, their presumed age readings were very poorly correlated with those of other structures and agreement was extremely low in all comparisons. A lack of any significant relationship between growth of either the fish or the dorsal fin spine with presumed spine age demonstrate that dorsal fin spines are not usable as an aging structure for spotted seatrout in the Chesapeake Bay region.

Scale agreement between the first and second readings of one reader was quite high in this study – 94%. This compares favorably to most reports by previous workers: Klima and Tabb (1959) – 91%, Moffett (1961) – 90%, Tabb (1961) – 92%, and Wakeman and Ramsey (1985) – 76%. In spite of this, inconsistencies in the marks of scales made age interpretation exceedingly difficult, and these inconsistencies lead to low reader confidence and relatively low agreement between different readers. Previous studies that aged spotted seatrout with scales reported similar problems. Wakeman and Ramsey (1985) noted that false annuli were often difficult to distinguish from true annuli, while Stewart (1961) noted partial marks, and that false marks were common. Many workers also have reported that large percentages of spotted seatrout scales were unusable for aging: Pearson (1929) reported 28.5% to be "unusable," Klima and Tabb (1959) called 13% "useless," Moffett (1961) had 11% that were "illegible," Stewart stated that 22% were "unsuitable," and Brown (1981) discarded 31% due to reader disagreement. Though these authors did not typically elaborate on the difficulties they encountered in scale reading, it is likely that their high percentages of unusable scales were due in part to inconsistencies like those reported here. Moffett (1961), Stewart (1961) and Tabb (1961) validated scale aging for ages 2 and 3 for Florida spotted seatrout. My results also indicated fairly good agreement between scale and otolith ages at age 2 and 3, however, when younger or older ages were considered, systematic disagreement between these structures was readily evident for spotted seatrout of the Chesapeake Bay. Inconsistent marks and the systematic tendency of scale ages to disagree with otolith ages (validated in Chapter 2) indicate that scales should not be used to age spotted seatrout of the Chesapeake Bay.

Sectioned otoliths were far superior to all other compared structures in all chosen criteria for aging spotted seatrout. Marks were clear, reader confidence was high, agreement was 100% both within and between readers, and both fish size and structure size increased significantly with otolith age. As such, sectioned otoliths were found to be the preferred aging structure for spotted seatrout of the Chesapeake Bay region.

Comparison of whole and sectioned otoliths

Though marks on whole otoliths were not as clear or as easy to read as those on sectioned otoliths, whole structures showed early promise as an alternative to sectioning. Overall percent agreement with sectioned ages was very high, and whole ages correlated well with sectioned ages. Though reader confidence in whole structure readings was low relative to sectioned readings, this was not of initial concern since 1) the density of the structure, 2) misleading surface features, and 3) the lack of magnification used in reading otolith sections would be expected to lead to lower confidence. However, since whole ages were shown to be different from sectioned ages (validated in Chapter 2), in both the t-test and a test of symmetry, we must conclude that whole otoliths should not be used to age spotted seatrout of the Chesapeake Bay region.

Chapter 2

Validation of presumed annual marks found on sectioned otoliths of spotted seatrout

Introduction

Many methods have been used to age fishes. These methods have typically relied on marks found on the various calcified structures of the fish to indicate age. Length-frequency analysis has also been frequently used to age a wide variety of species but workers repeatedly have found this method ineffective for spotted seatrout because sizes at age overlapped so much that age groups were not clearly evident (Pearson, 1929; Moody, 1950; Tabb, 1961; Wade, 1981; Wakeman and Ramsey, 1985). Of the calcified structures used to age fishes, only scales and otoliths have found much use for spotted seatrout. Most aging studies for this species have used scales (Pearson, 1929; Miles, 1950; Klima and Tabb, 1959; Moffett, 1961;Stewart, 1961; Tabb, 1961; Iversen and Tabb, 1962; Brown, 1981;Wade, 1981; Rutherford, 1982; Colura et al., 1984; Wakeman and Ramsey, 1985), while others have employed sectioned otoliths (Sundararaj and Suttkus, 1962; Miles, 1951; Maceina et al., 1987; Murphy and Taylor, 1994; Wenner, 1997).

Unfortunately, few attempts have been made to validate these aging methods. To be useful, an aging method must accurately reflect calendar age of the animal. The process of assessing accuracy of age estimates is termed “validation.” Beamish and McFarlane (1983) have demonstrated that the use of unvalidated ages can lead to dangerous and costly mistakes in fisheries management. Moreover, Beamish and McFarlane and others (Williams and

Bedford, 1974; Chilton and Beamish, 1982; Casselman, 1983) point out that the aging methodology should be validated for each age and each population since the appearance of annuli can vary with both age and geographical differences.

Scale ages have been validated in the South only for ages 2, 3 and 4 (Moffett, 1961; Stewart, 1961; Rutherford, 1982; Colura et al., 1984) but scale aging has been applied to presumed ages to 15+ in the Chesapeake Bay (Brown, 1981) – a region where scale aging has never been validated for any age. Ihde (Chapter 1) compared otoliths, scales, fin rays and spines of Chesapeake Bay spotted seatrout and found otoliths to be superior to the other structures for clarity and ease of aging this species in the Chesapeake Bay. Otoliths have been validated in Texas (Maceina et al., 1987) and Florida (Murphy and Taylor, 1994), however, validation still has not been performed anywhere north of Florida. Thus, the present study validates the use of sectioned otoliths for aging spotted seatrout of the Chesapeake Bay region, for as many ages as possible, using an anatomical method of validation known as marginal increment analysis (MIA).

Methods

Fish collection

A total of 2763 spotted seatrout were collected June 1996 to March 1999 from commercial haul-seine and gill net catches. The fish were primarily from the Chesapeake Bay (96.7%), but Bay catches (n = 2448) were supplemented with fish from near Cape Hatteras, North Carolina (n = 315) during the months of November to April for MIA, when few spotted seatrout were available in the Chesapeake Bay. I assumed that fish from the Chesapeake Bay and fish from North Carolina's winter fishery had very similar marks on their otoliths and may well be from the same population. That assumption is probably well founded, because 1) Bain et al. (1998) reported that a 394 mm seatrout tagged inside the Chesapeake Bay in September was recaptured off Nags Head, NC the following May, and 2) H.C. Yarrow (*In* Goode, 1884) reported that spotted seatrout migrate seasonally: north from North Carolina waters about May – possibly as far north as Long Island – and south from northern waters around September – possibly as far south as northeast Florida.

Processing procedures

Each fish was measured for standard length (SL), total length (TL), total weight (TW), and eviscerated weight (EW). Torn or damaged caudal fins were common; so all calculations are based on SL, unless otherwise noted. TL values reported in this study were predicted from the following TL – SL relationship observed in 1357 fish:

$$TL = 10.56 + 1.1537 * SL \qquad (100\ r^2 = 99.5\%)$$

Sagittal otoliths were removed from each fish, wiped, and stored dry. A size-stratified subsample of fish (n = 683) was randomly selected (SAS, 1991) each month from my total catch (following Bagenal and Tesch, 1978) to validate the sectioned otoliths method by MIA. All fish were included in the subsample if less than 20 fish were collected in any month. If more than 20 fish were collected in any month, however, the subsample was made up of: 15% of the fish smaller than 450 mm (n = 245), 30% of fish 450 - 701 mm (n = 414), and all of the fish 702 mm TL or larger (n = 24).

The right or left otolith was randomly selected and transversely sectioned as described in Chapter 1. Significant difference between left age and right age was tested for with the Mann-Whitney test (Wilcoxon rank sum test) (SAS, 1989a; Zar, 1996).

Aging was done in transmitted light. I interpreted the distal edge of the translucent growth band (≡ proximal edge of the opaque band) as a completed presumed annual mark (Williams and Bedford, 1974; Casselman, 1983). The annual mark in Chesapeake Bay region spotted seatrout consists of a bipartite set of bands, a narrow opaque band formed in early summer and a wide translucent band formed over the rest of the year. The main counting paths used in aging were the ventral and dorsal arms of the sulcal groove (Fig. 12). A mark had to be complete in both of the main counting paths before it was considered a presumed annular mark

Marginal increments (MI's) – the growth on the otolith since the last completed mark – were measured as the distance from the distal edge of the last translucent band to the edge of the otoliths section (Fig. 13) using a compound microscope equipped with a calibrated Optimas® image analysis system. All measurements were made along the ventral arm of the sulcal groove, in random order without knowledge of fish size or collection date.

A one-way analysis of variance (F-test) was used to determine if there was a significant difference in MI's among months. Differences between individual months were then examined for each presumed age group, using monthly plots of MI frequencies. Presumed age groups were based on the number of presumed annual marks observed on sectioned otoliths.

The sectioned otoliths aging method was considered valid, and mark formation was termed "annual," if one presumed annual mark was formed each year, for each age group (frequency), at a similar time of year for all ages (timing).

Frequency was evaluated by: 1) how many times a year a new mode appeared in MI frequency plots – a new mode was composed of individuals that had just formed a new mark and subsequently demonstrated extremely small MI's. Typically, during the month(s) a new mode appeared, individuals that had not yet formed a mark were still present in a second mode of relatively large MI's, thus, months of mark formation were usually indicated by a bimodal MI frequency distribution – and by 2) the occurrence of "0" MI's in plots of percentage 0 MI's by month. A "0 MI" was defined as an otolith section that had a continuous, extremely narrow opaque margin (the margin of an otolith section called "0 MI" never exceeded 8.9 x10^{-2} mm) that defined the distal edge of the translucent band.

Timing was evaluated using these same plots, to establish whether or not all age groups formed a mark at the same time of year, each year.

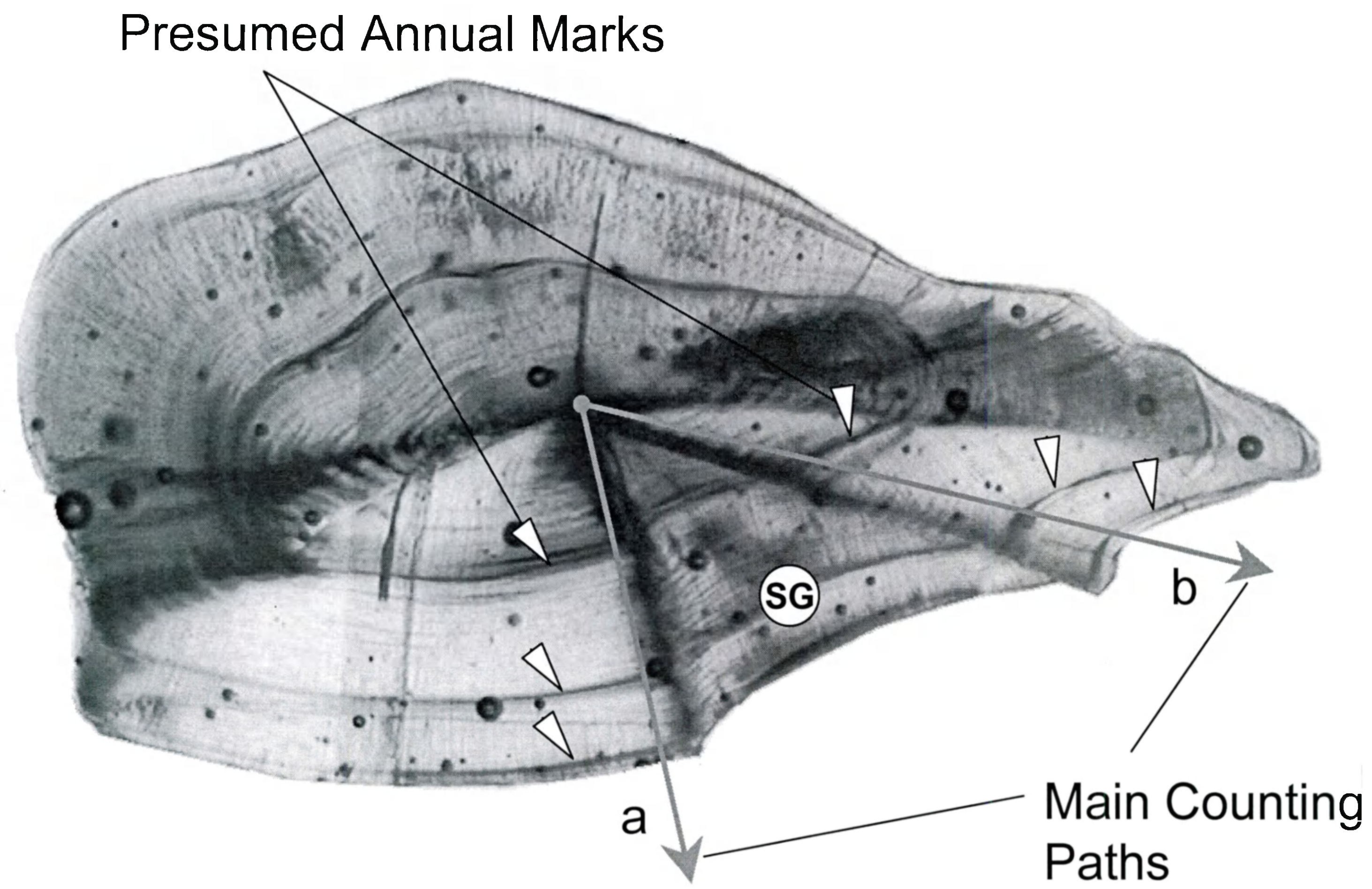
Annual mark formation can be most conclusively shown when: 1) a new mode of very small MI's is formed, 2) that mode can be followed throughout the year as the increments grow in size, and finally, twelve months later, 3) the mode (now composed of large increments), co-occurs with a new mode of small increments.

Timing of the first mark

To show that the first visible mark actually forms during the first year of life, otoliths of young-of-the-year (YOY) spotted seatrout caught monthly in the Chesapeake Bay from July to November 1998 were transversely sectioned as described in Chapter 1. The appearance of the presumed sub-annual marks and size of the otolith cross-sections were then compared to those of presumed age 1+ fish. The first visible mark was considered to actually form during the first year of life if the presumed sub-annual marks and otolith cross-sections were consistent with those of the presumably slightly older age 1+ fish.

Rejection of the null hypothesis was based on $\alpha = 0.05$ for all statistical tests. In all instances, "P" refers to probability, "z" refers to the normal deviate, and SE stands for standard error. When P is given alone, it refers to the probability of observing a greater F-value in an F-test.

Figure 12. An otolith section of an age 3 spotted seatrout, with 3 presumed annual marks indicated by the arrowheads. These marks are each complete in that they are present in both main counting paths, the ventral (a) and dorsal (b) arms of the sulcal groove (SG).


Presumed Annual Marks
SG
b
a
Main Counting Paths

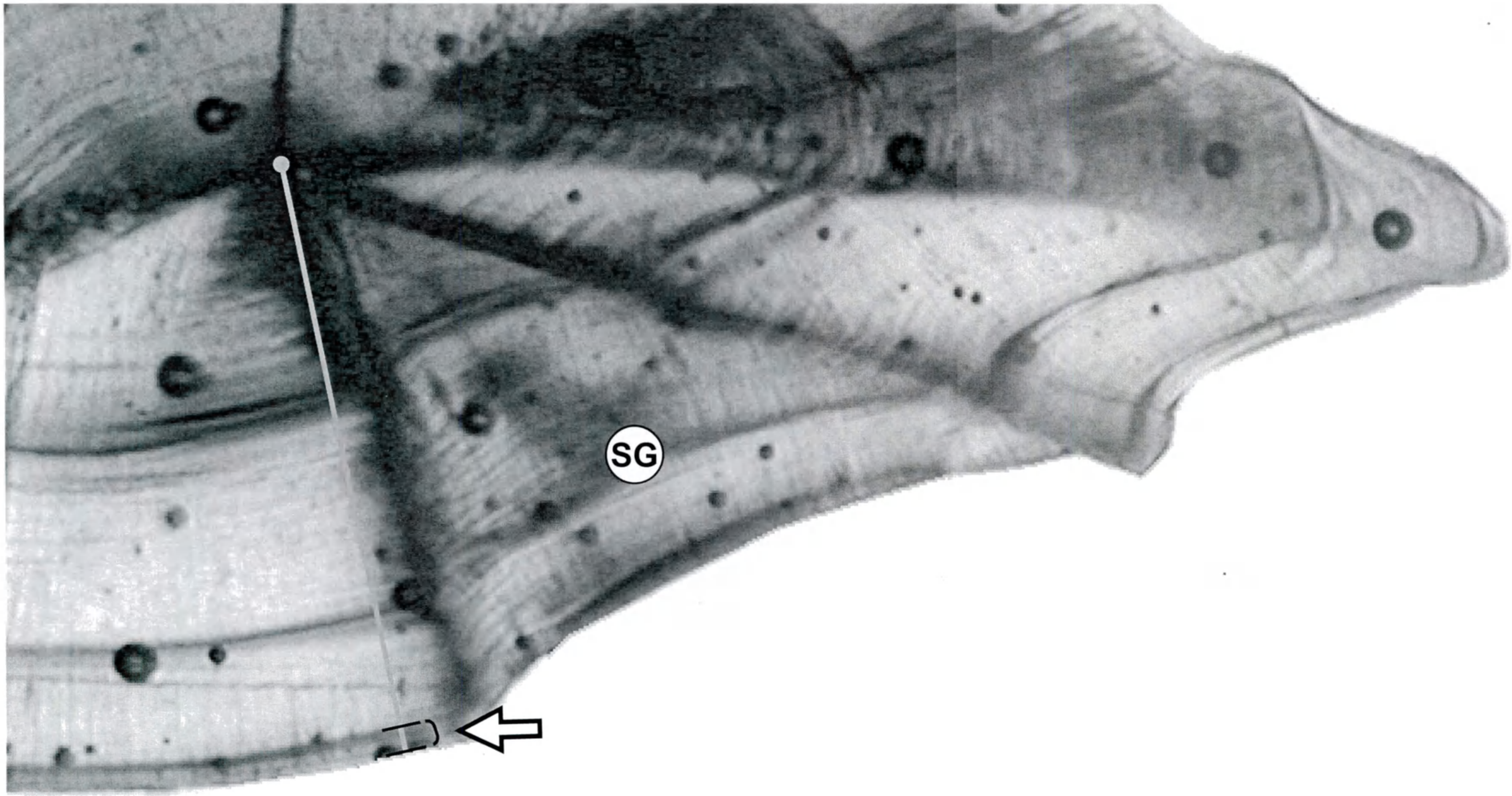


Figure 13. The marginal increment (indicated by arrow) is the distance (in mm) from the distal edge of the last translucent band to the edge of the otolith section. All measurements were made along the ventral arm of the sulcal groove (SG) as indicated by the line.

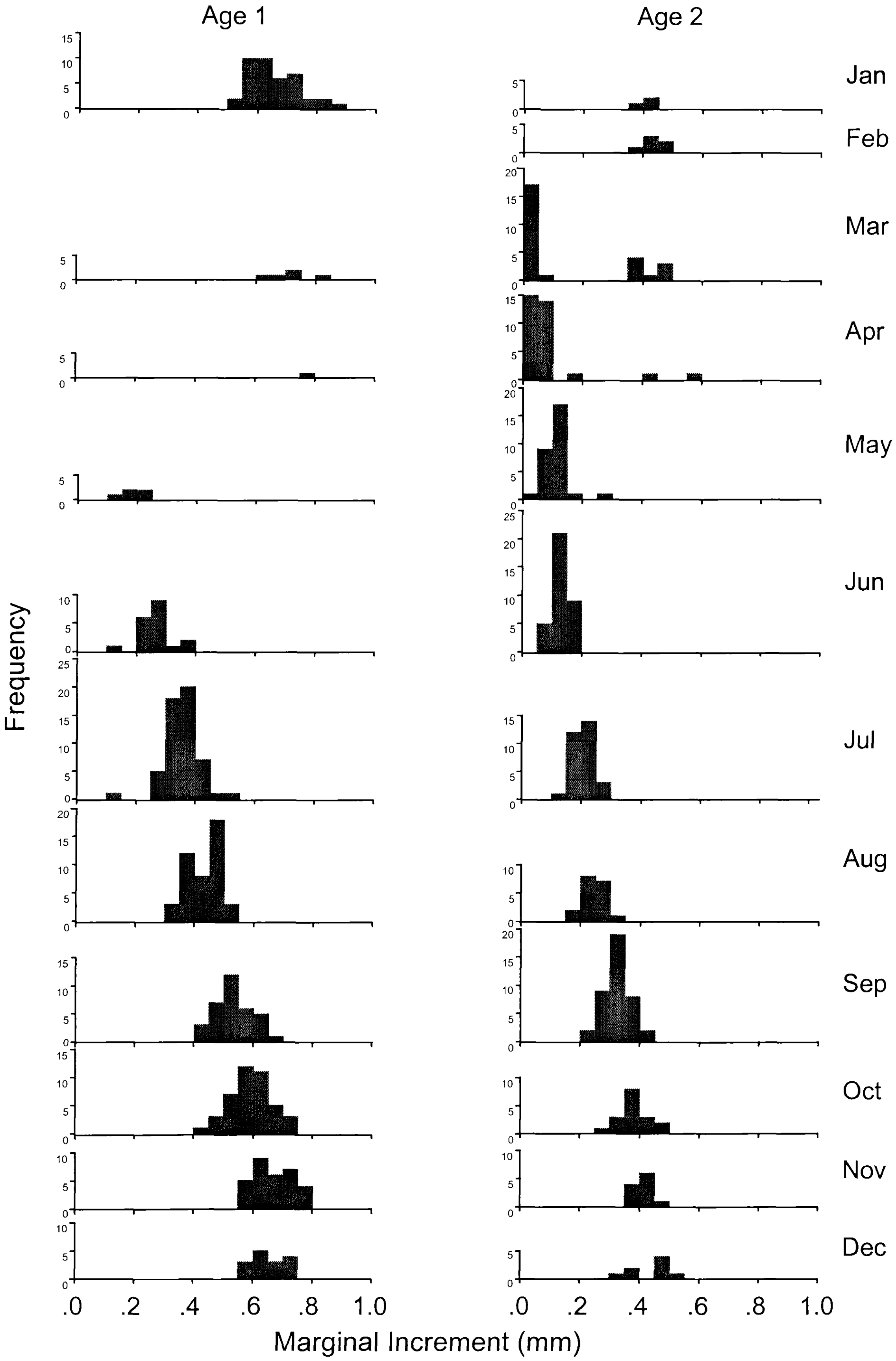
Results

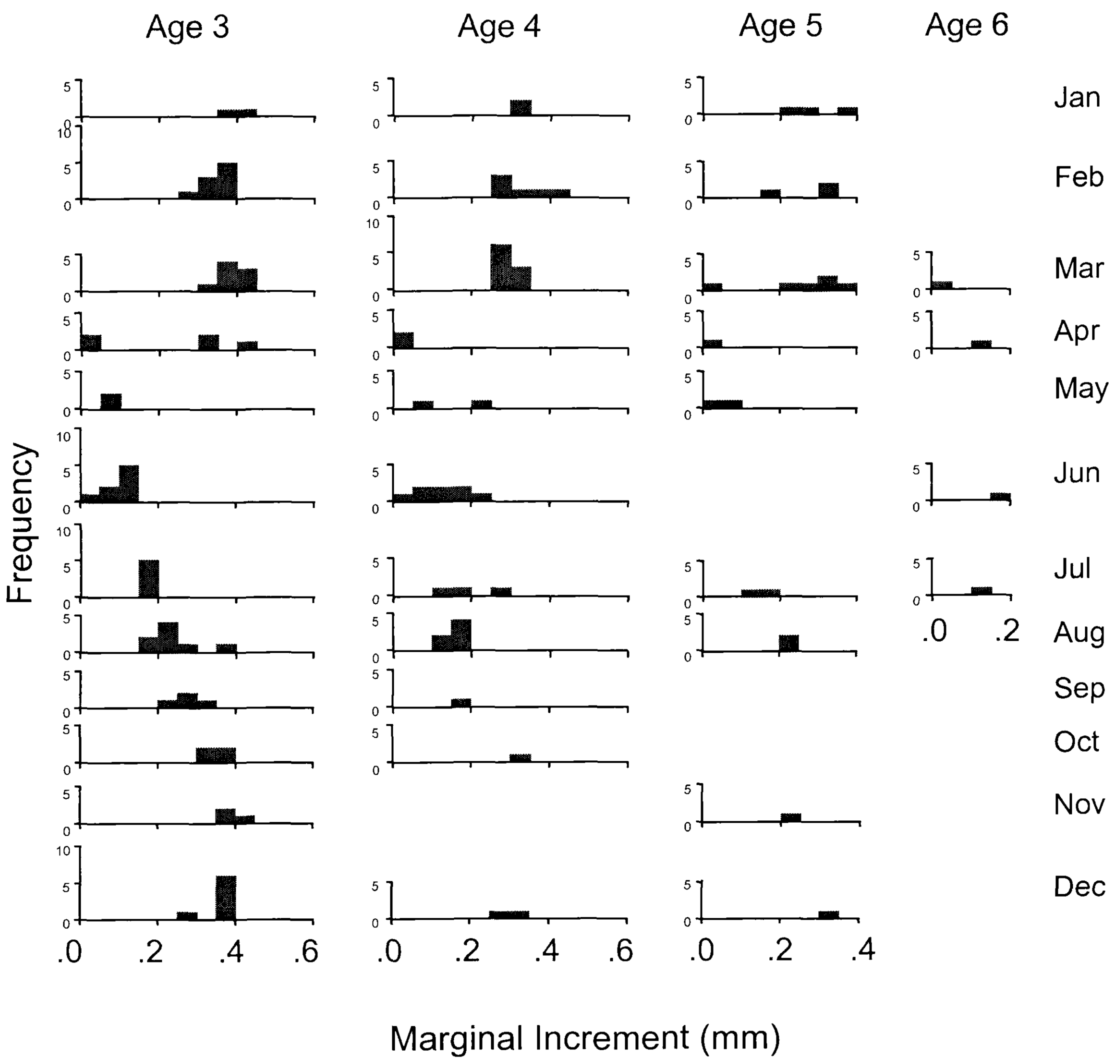
There was no significant difference in ages between left and right otoliths ($P > |z| = 0.200$). One-way ANOVA however, found highly significant differences in marginal increments among months ($P < 0.0001$).

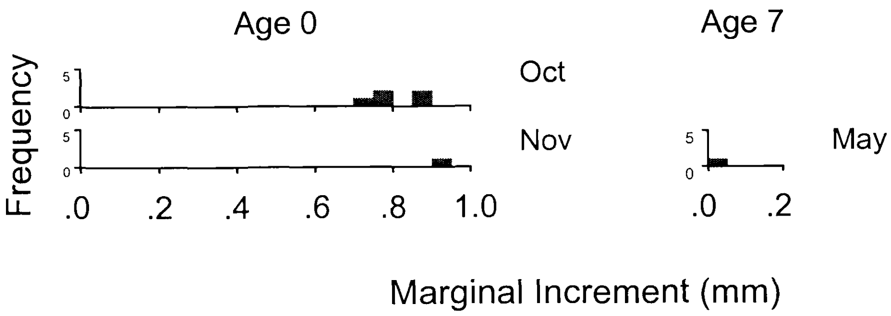
Annual marks are formed on spotted seatrout otolith sections once a year in the Chesapeake Bay region, during the months of March and April. For ages 1 – 5, monthly MI frequency plots were typically unimodal (Figs. 14 – 15), and the progression of the mode was easily followed over long periods of time (i.e. May through November) as the increments grew in size. The MI mode reached its maximum size in November, and generally remained stable (indicating very slow winter otolith growth in this region) through March or April, when rapid otolith growth resumed. A new mode of very small increments appeared in all ages (1 – 5) during March and/ or April, which indicated many individuals had formed a new mark during these months. Additionally, March and April were the only months in which 0 MI's occurred (Fig. 16). This consistent pattern of MI growth conclusively indicated 1) the frequency of mark formation was once a year, and 2) the timing of mark formation in the Chesapeake Bay region was restricted to the same short time period each year – during March and April.

Marginal growth decreased rapidly with age. Though patterns of growth remained consistent between ages, it was quite noticeable that annual margin

Figures 14 – 15. Monthly marginal increment frequencies by age for spotted seatrout.


Age 1
Age 2
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Frequency
0
5
10
15
20
25
.0
.2
.4
.6
.8
1.0
Marginal Increment (mm)


Age 3
Age 4
Age 5
Age 6
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Frequency
0
5
10
.0
.2
.4
.6
Marginal Increment (mm)


Age 0
Age 7
Oct
Nov
May
Frequency
0
5
.0
.2
.4
.6
.8
1.0
Marginal Increment (mm)

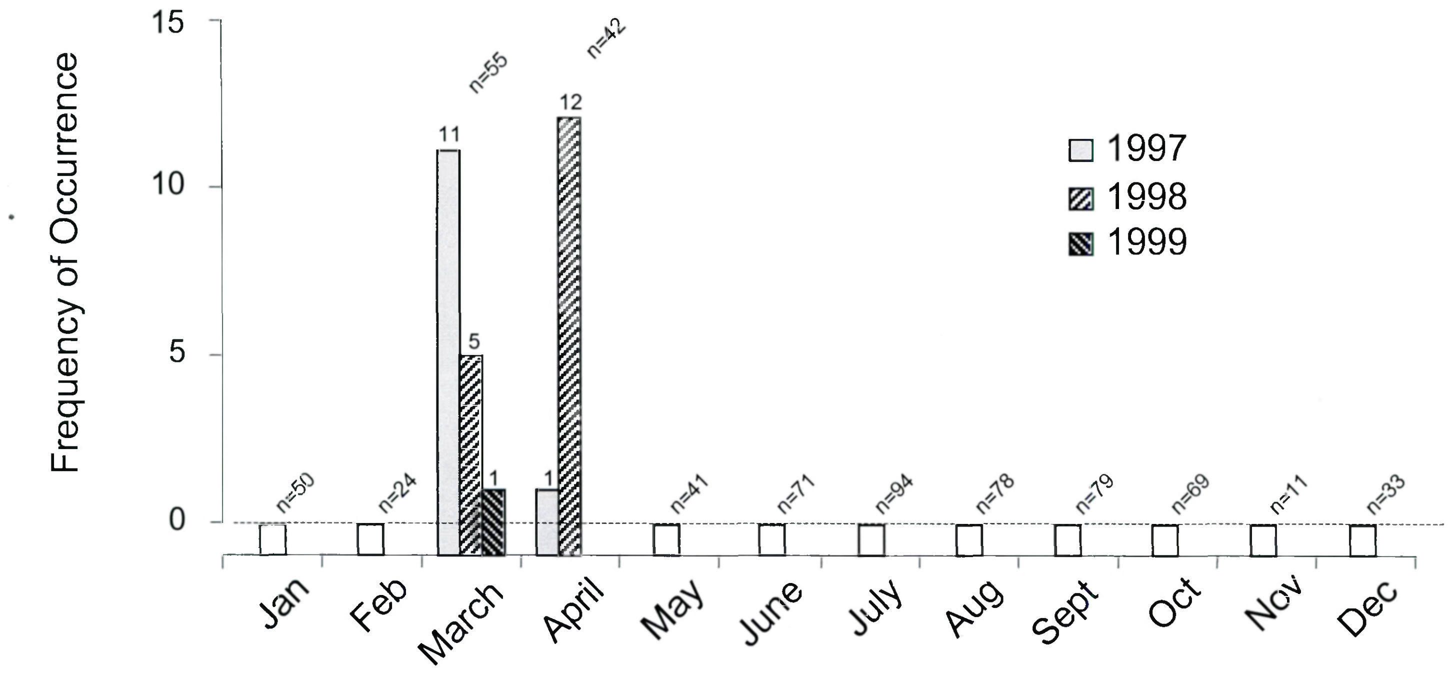


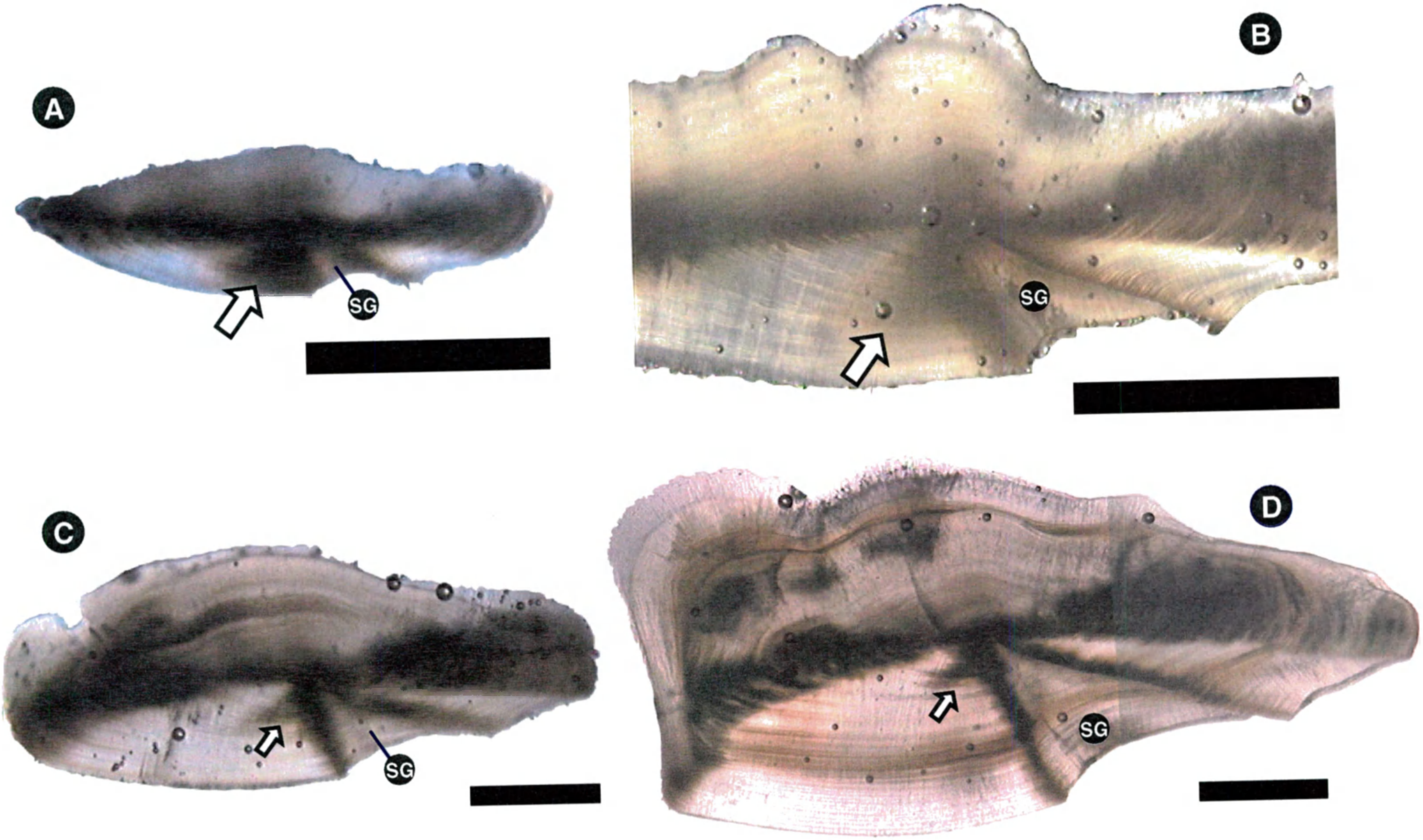
Figure 16. Monthly occurrence of "0" marginal increments for spotted seatrout. Numbers above each bar (n = __) represent the number of fish examined that month for otoliths with 0 marginal increment. The additional numbers above each year bar represent the number of 0 marginal increments observed.

growth slowed drastically after age 1. This fact was readily apparent when maximum margin growth of age 1 fish (about 0.8 mm) was compared with that of ages 3 – 5 fish (about 0.4 mm). Maximum margin growth attained for age 1 fish was about twice that attained for ages 3 – 5 fish, while the maximum margin growth of age 2 fish was intermediate at about 0.6 mm.

Though too few fish were captured to validate the sectioned otolith method for ages 0 (n = 6), 6 (n = 4) and 9 (n = 1), the marginal increments observed follow the same pattern as ages 1 – 5 fish in important respects: 1) a 0 MI for an age 6 fish was observed in March, 2) margins showed growth from March through July for age 6 fish, and 3) the overall pattern of decreasing margin growth with age was even more evident at the age extremes observed – age 0 fish showed greater yearly margin growth to November than any other age group, the otolith margins of age 6 fish were most similar in size to ages 3, 4 and 5, and the only age 9 fish caught had an extremely small, but well defined margin, that showed the annual mark had formed well before capture in May.

The first visible mark on the spotted seatrout sectioned otolith is formed during the first year of life. Both 1) the size and shape of the sub-annual marks and 2) the size and shape of otolith cross-sections of YOY fish directly correspond to those of presumed age 1+ fish at their first mark. A roughly triangular sub-annual mark appeared in all otoliths sectioned. This opaque mark extends from the nucleus of the otolith, hence, it appears to form very early in life, probably from the time of hatching. The triangular mark appeared along the ventral arm of the sulcal groove and disappeared about late July in my YOY otolith sections (Fig. 17a.), and apparently corresponded to a short period of rapid early growth of the otolith. The shape and size of this mark are nearly identical for YOY fish captured in late fall (Fig. 17c.) and presumed age 1+ fish caught during the following year (Fig. 17d.). Further, it can be readily seen that the MI size (October – November YOY MI ranged 0.62 – 0.83 mm; see Fig. 18) and the shape of a typical late fall YOY otolith section are nearly identical to the size and shape of an older fish's otolith section *at* its first mark (mean MI of age 1+ fish = 0.81; 0.0054 mm SE; n = 242). These similarities could only occur 1) if the YOY otolith growth is slow over winter months (as it is for ages 1-5) and 2) if the first mark is formed when rapid growth resumes during the first spring of life. Thus, it was inferred that the first mark was formed during the first year of life for spotted seatrout of the Chesapeake Bay region.

Figure 17. Appearance and size of young of the year (YOY) (A, B, C) and presumed age 1+ (D) otolith sections of spotted seatrout. Note the early opaque triangular mark (TM) (indicated by arrows) observed along the ventral arm of the sulcal groove (SG) in all otolith sections. A) Otolith from an 82 mm TL YOY, collected in late July, the smallest fish sectioned. Note TM appears complete in this section. B) TM formation has clearly ended prior to early September when this YOY was caught. C) YOY otolith section collected the end of October. Note the similarity in size and shape of otolith section C to section D at D’s first annual mark. (Scale bar marks are 1mm.)


A
SG
B
SG
C
SG
D
SG

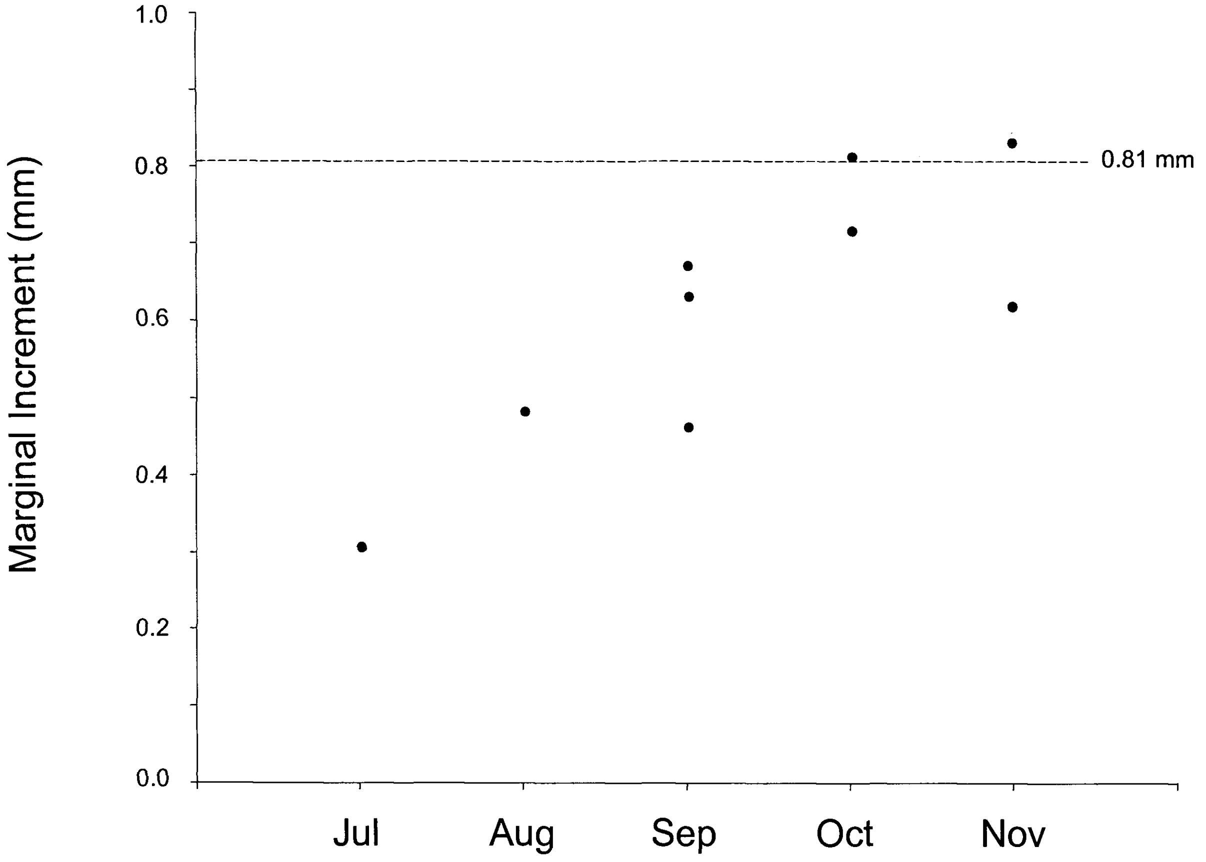


Figure 18. Marginal increments of young-of-the-year spotted seatrout compared to the mean marginal increment (dashed line) of the first mark on all presumed age 1+ fish (n = 242; 0.0054 mm SE).

Discussion

The sectioned otolith aging method was considered to be valid for age 1 – 5 spotted seatrout in the Chesapeake Bay region because annual marks form once a year, at the same time each year. The sectioned otolith aging method has been previously validated for ages 1 – 5 in Texas by Maceina et al. (1987) and for ages 1 – 3 in Florida by Murphy and Taylor (1994). Like Maceina et al. (1987), I found that the timing of annual mark formation in sectioned otoliths was limited to March and April. Although Murphy and Taylor (1994) reported much more variable timing of mark formation for this species in Florida (between November and May), their results do not disagree with those presented here. It is possible that examining the monthly marginal increment frequency distributions by age for bimodality could help further resolve specific months of mark formation in studies like Murphy and Taylor's, where mean, minimum and maximum marginal increment values proved inadequate to resolve the timing of mark formation.

As a result of these three studies, sectioned otoliths have now been validated over 1) the most commonly observed ages – 1 to 5, and 2) over the extremes of the spotted seatrout's U.S. range – Texas in the south, Florida in the middle, and Virginia in the north.

Chapter 3

Reproductive life history, age and size composition, growth and mortality of Chesapeake Bay spotted seatrout

Introduction

For nearly three centuries, the spotted seatrout, *Cynoscion nebulosus*, has been recognized as a high quality food fish (Lawson, 1709 *in* Smith, 1907; Goode, 1884; Hildebrand and Schroeder, 1928; Pearson, 1929; Hildebrand and Cable, 1934; Brown, 1981; Mercer, 1984). Consequently, the spotted seatrout has been heavily fished, both commercially and recreationally, throughout its U.S. range, from Delaware Bay to Texas (Welsh and Breder, 1923).

Much work has been done on the commercially and recreationally important Sciaenids of the Middle Atlantic coast (Smith, 1907; Perlmutter et al., 1956; Merriner, 1976; Wilk, 1979, 1981; Cato, 1981; Weinstein, 1981; Shepherd and Grimes, 1983; Ross, 1988; Lowerre-Barbieri et al., 1995; Barbieri et al., 1994). Much work has also been done on spotted seatrout, including: reproduction (Tabb, 1961; Sundararaj and Suttkus, 1962; Mahood, 1975; Hein and Shepard, 1979; Brown, 1981; Brown-Peterson and Thomas, 1988; Colura et al., 1988), larval growth and development (Fable et al., 1978; Peebles and Tolley, 1988), juvenile life history (McMichael and Peters, 1989; Rutherford et al, 1989a), food habits (Overstreet and Heard, 1982; Hettler, 1989), parasitology (Overstreet, 1977; Collins et al., 1984), endocrinology (Smith and Thomas, 1990), environmental requirements (Perret, 1971; Wohlschlag and Wakeman, 1978; Vetter, 1982), culture (Bumguardner et al., 1992; Porter and Maciorowski, 1984; Gray et al., 1991), economic value (Cato, 1981), sound production (Mok and Gilmore, 1983; Saucier and Baltz, 1993), movements (Iversen and Tabb, 1962; Baker et al., 1986), stock identification (Weinstein and Yerger, 1976; Ramsey and Wakeman, 1987; King and Pate, 1992; Gold et al., 1999), aging and validation (Moffett, 1961; Colura et al., 1984; Maceina et al., 1987; Murphy and Taylor, 1994; Chapter 2), growth (Pearson, 1929; Moffett, 1961; Colura, et al., 1984), and mortality (Wakeman and Ramsey, 1985; Rutherford et al., 1989b; Murphy and Taylor, 1994). However, little work has been directed to east coast populations, and very little is known about age structure, growth, reproduction and mortality north of Georgia.

Since growth of this spotted seatrout may vary latitudinally as it does in the closely-related weakfish *Cynoscion regalis* (Shepherd and Grimes, 1983), proper management requires that accurate age, growth, reproduction and mortality information be assessed throughout its range. The only information recorded, however, on the spotted seatrout populations north of Georgia to date is found in: 1) second-hand accounts of H.C. Yarrow's cursory observations of the North Carolina fishery from more than 100 years ago (Goode, 1884; Smith, 1907; Hildebrand and Schroeder, 1928); 2) an educational booklet for South Carolina's recreational fishermen (Wenner, 1997), and 3) Brown (1981), who addressed age, growth and reproduction in the Chesapeake Bay. Unfortunately, Brown used only a small sample of spotted seatrout, and she based her study on unvalidated scale-aging, which has since been shown to be an unreliable aging method in this region (Chapter 1). Accurate age, growth, reproduction and mortality information is still needed for management in this region, so, the objectives of this study were to describe 1) spawning periodicity, 2) age composition, 3) size composition, 4) growth, and 5) mortality for the spotted seatrout found in the Chesapeake Bay.

Methods

Sampling

A total of 2448 spotted seatrout were purchased from Chesapeake Bay commercial fishery catches June 1996 - March 1999. My initial goal was to obtain fortnightly a 22.7 kg (50 lb) box of each available grade from each of six locations around the Bay (see Chapter 1, Fig. 1). However, it soon became apparent that catches of spotted seatrout were too sporadic to meet this goal. Therefore, beginning May 1997, the goal was modified to obtain 150 fish per month from any source possible. Fish from location 4 were available regularly, and fish from locations 5, 6 and 7 were available in winter months. Typically I obtained total catches -- ungraded -- from commercial haul-seine fishermen. When graded catches were available (34.4% of all fish), a 22.7 kg (50 lb) box of each available grade was purchased (small, medium or large), and total weights for all available grades were recorded if possible. Though boxes were not randomly selected, Chittenden (1989) found that in the haul-seine fishery, nearly all variation in catch composition was associated with within-box variation, so each graded box purchased was considered representative of that grade.

Each fish was measured for standard length (SL), fork length (FL), total length (TL), girth (G), total weight (TW), gonad weight (GW) and eviscerated weight (EW). Torn or damaged caudal fins were common, so calculations are based on SL unless otherwise noted. Sex was recorded, and ovaries were macroscopically staged as described below. Sagittal otoliths were removed, wiped clean, and stored dry.

Reproduction

Analysis of spawning periodicity was based on 1) the gonadosomatic index (Crim and Glebe, 1990) [calculated as: GSI = (Gonad Weight/ EW) * 100] of all Chesapeake Bay fish that were sexed (n = 2297), and 2) the macroscopic stages of all spotted seatrout ovary pairs that were collected (n = 995). Eviscerated weight was used to calculate GSI instead of total weight because spotted seatrout often swallowed extremely large prey compared to their body size. This undigested food greatly affected total weight, thus eviscerated weight better estimated somatic weight.

Macroscopic stages were based on the descriptions of Tabb (1961) for spotted seatrout and Lowerre-Barbieri et al. (1996) for the closely related weakfish, and were as follows:

1) Immature: ovaries very small, translucent – ribbon-like;
2) Developing: ovaries small to medium (≤ 25% of body cavity) light orange, no oocytes visible;
3) Fully Developed – ovaries large (50-75% of body cavity); pale yellow in color, opaque oocytes prevalent, little ovarian vascularization and no sign of previous spawning – granular appearance;
4) Partially Spent / redeveloping: ovaries medium to large (30-50% of body cavity) somewhat flaccid, orange – may be some remnant hydrated oocytes;

5) Gravid: ovaries extremely large (100% of body cavity) hydrated oocytes easily seen – speckled granular appearance;

6) Running Ripe: similar to gravid, but ovary size variable – medium to large, eggs can be extruded with gentle pressure to abdomen;

7) Regressing: ovaries flaccid and small (< 20% of body cavity), color variable - yellow to orange to maroon, may contain a few visible oocytes;

8) Resting: ovaries small and dense, dark orange to maroon in color, no visible oocytes, ovarian membrane thickened and more opaque than Immature stage.

Age and length at 50% and 100% first maturity were determined by probit analysis (SAS, 1989b) of percent mature female spotted seatrout (representing all macroscopic gonad stages except "Immature") against age (in years) and length (in mm), respectively. Age and length at first maturity was also described for females, based on the youngest and smallest individual(s) aged with "Fully Developed" ovaries.

Age determination

Preliminary examination indicated that about 82% of the fish collected were age 2 or less (Chapter 1), so, a random size-stratified subsample was selected for aging as described in Chapter 2.

The right or left otolith was randomly chosen (by coin toss) and transversely sectioned. The number of annual marks was determined in transmitted light by counting the number of completed translucent bands present in each section, since these bands represent the "winter" slow growth period in the bipartite annual mark (Williams and Bedford, 1974; Casselman, 1983). Annual marks were consistently visible along the ventral and dorsal arms of the sulcal groove, so these paths were used for counting (see Chapter 2, Fig.12). Magnifications up to 1000x were employed to interpret the otolith edge during March and April, the months of annulus formation (Chapter 2). Age equaled the number of annual marks observed.

Age composition

All Chesapeake Bay fish aged (n = 661) were used to describe the observed minimum and maximum age. The mean and standard error of spotted seatrout age were determined with 1) all fish aged and 2) an expansion of fish available from the Chesapeake Bay commercial fishery (n = 19,193; expansion is described below).

Age at the end of the fishable life span, "t_L" was described using 1) the oldest fish observed and the age that described 2) 99% and 99.5% of all fish (i.e. the age at which 1% and 0.5% of the fish remain, respectively). 99 and 99.5 percentiles were calculated for both 1) all fish actually aged and 2) all fish estimated to be available by expansion. Age composition of fish aged was compared among years, by right/ left otolith and by sex with the Wilcoxon rank sum test (a.k.a. Mann-Whitney U test) (Zar, 1996; SAS, .1989a). Only aging data from 1997 and 1998 were used for comparing ages among years since fish were collected nearly every month in these years, but only sporadically in 1996 and 1999.

Expansion of fish available from the Chesapeake Bay commercial fishery

Since fish were selected for aging by a random size-stratified subsample of all fish purchased, and since purchased fish were from both total catches and partial catches (i.e. commercially graded partial catches), observed number at age was expanded to estimate the number of fish at age available from the Chesapeake Bay commercial fishery. Expanded estimates were then used to calculate mean age, t_L, and t′ (by catch curve analysis, see below), for comparison to values obtained from the raw data. Number observed at age was expanded according to the following formula:

$$\begin{array}{l}\text{Expanded no. of}\\ \text{fish at age "z"} = b_{G_1}(\bar{n}_{G_1S_1} * P_{S_1} + \bar{n}_{G_1S_2} * P_{S_2} + \bar{n}_{G_1S_3} * P_{S_3}) + b_{G_2}(\bar{n}_{G_2S_1} * P_{S_1} + \bar{n}_{G_2S_2} * P_{S_2} + \ldots) + \ldots\end{array} \quad (1)$$

where:

$z =$ each observed age

$$b_{G_x} = \frac{\text{No. of commercial}}{\text{grade "x" boxes landed}} \Big/ \frac{\text{No. of commercial grade}}{\text{"x" boxes purchased}}$$

$$b_{G_x} = \frac{\text{No. of commercial}}{\text{grade "x" boxes landed}} \Big/ \frac{\text{No. of commercial grade}}{\text{"x" boxes purchased}}$$

$$n_{G_xS_y} = \text{observed in grade "x"} \Big/ \text{boxes purchased}$$

size "y" = an arbitrary size class of fish, i.e. either 1) small -- smaller than 450 mm,
2) medium -- 450 - 701 mm, or 3) large -- 702 mm TL or larger.

$$P_{S_y} = \frac{\text{No. of age "z" fish observed}}{\text{from size "y" in all grades}} \Big/ \frac{\text{No. of fish aged from}}{\text{size "y" in all grades}}$$

Only Chesapeake Bay fish collected on or after May 1 were used in this expansion. This ensured that fish of the same biological year were aged together, since all fish had formed a new annual mark on their otoliths prior to

May 1 (Chapter 2). The expansion was limited to data from 1997 and 1998 since fish were collected nearly every month in these years, but only sporadically in 1996 and 1999.

Size composition

All 2448 fish collected from the Chesapeake Bay were used to describe maximum, minimum, mean and standard error of fish size. Size at the end of the fishable life span l_L was described using 1) the longest fish observed, and 2) the lengths representing 99% and 99.5% all fish. Length distributions were compared between the sexes with the Wilcoxon rank sum test (Zar, 1996; SAS, 1989a).

Length - length and length – girth relationships were determined by linear regression, and length - weight relationships were determined by linear regression with log transformation (SAS, 1990) and by simple quadratic regression. Significant differences between sexes for the linear regression relationships were tested for with ANCOVA (Zar, 1996; Littell et al., 1991).

Growth

Growth data were estimated for both ages in fractional years and ages in years.

To estimate growth using age in fractional years, mean size at age was described using all fish aged in a randomly selected size-stratified subsample of all fish collected from the Chesapeake Bay. Growth parameters were then determined by fitting fish length at capture to age of the fish in fractional years (see estimation procedure below). This was done using 1) a von Bertalanffy growth model (Ricker, 1975),

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad (2)$$

fitted by nonlinear least squares regression (S-PLUS, 1999) and, for comparison, 2) a seasonal von Bertalanffy growth function described in Longhurst and Pauly (1987),

$$L_t = L_\infty(1 - e^{-[K(t-t_0)+C*\frac{K}{2\pi}\sin 2\pi(t-ts)]}) \qquad (3)$$

and fitted also by nonlinear least squares regression (S-PLUS, 1999).

where:

L_t = length at age t

L_∞ = hypothetical maximum mean length

k = Brody growth coefficient

t = estimated age (or time) in fractional years

t_0 = hypothetical age at size zero if fish had always grown according to the equation

C = constant between 0 (where seasonal changes in growth are slight, like in the tropics) and 1 (where seasonal changes in growth are dramatic, like in the temperate Chesapeake Bay)

ts = elapsed time between hatching and onset of the first seasonal change in growth

According to Pauly (1984) the application of a seasonal curve should improve the accuracy of von Bertalanffy parameter estimates. Fractional age used for both the standard and seasonal von Bertalanffy growth models were based on an assumed birthdate of May 1 each year. To estimate fractional year age, I first aged the fish in years. I then assigned fractional year age to equal the number of annual marks observed plus the fraction of: the number of days passed from

May 1 until the day of capture, divided by 365. Because "ts" was estimated by a combination of size at age (in years) and size at time of capture (in fractional years), this time parameter estimate should be viewed with caution. May 1 was chosen as a standard birthdate for Chesapeake Bay spotted seatrout because: 1) all fish have formed a new annual mark by this date (Chapter 2), and 2) the first week in May appears to be the onset of the spawning season, (according to GSI results, see Fig. 19). In the seasonal function, C was assumed to equal 1. A C value of 1 would be expected in distinctly temperate waters and assumes that the growth rate is zero for a short period (less than several weeks) once each year (Pauly, 1984) – a realistic assumption for Chesapeake Bay spotted seatrout, since, as Murdy et al. (1997) point out, the "Chesapeake Bay has one of the most extreme annual temperature ranges known for coastal ecosystems in the world." Young-of-the-year (YOY) fish were excluded from the fitted curves, as suggested by Ricker (1975, p. 225), since the growth of YOY fish does not conform to the growth curve established by older fish.

To estimate growth using age in years, all fish purchased during April 1998 (n = 104) were aged and ages in years were fit separately to the standard von Bertalanffy growth model, using nonlinear least squares regression (S-PLUS, 1999). Growth parameters based on annual ages were thereby estimated for comparison with parameter estimates based on assigned daily ages. Only one month – April – was chosen for this comparison in order to minimize the variation of length at each age. April was chosen because 1) it is the last month of annual mark formation, so all otoliths were either forming a mark or had already completed one – consequently, there was no confusion as to the appropriate biological year when aging and 2) there was a wide size range of fish available this month.

Mortality

The instantaneous rate of total annual mortality (Z) was estimated in four ways, using all fish collected from the Chesapeake Bay, by:

1) Beverton and Holt's (1956) length-based Z equation:

$$Z = \frac{k\,(L_\infty - \bar{l})}{\bar{l} - l'} \tag{4}$$

where:

L_∞ and k were estimated using the standard von Bertalanffy model as applied to all fish aged from the Chesapeake Bay by the method described above, and:

l' = smallest length of fish that are fully represented in catch samples

$\bar{l}$ = the mean length computed from l′ upwards

as described by Beverton and Holt (1956). The smallest length fully represented in the catch, "l′ " corresponds to a given "t′." t′ was estimated to be age 2 by catch curve analysis (described below), so l′ was interpreted to equal the mean length of the observed 2 year olds (495 mm TL).

2) Hoenig's (1983) maximum age-based pooled regression equation:

$$Z = e^{1.44 - .98\, t_{max}} \tag{5}$$

where: t_{max} is the maximum age as determined by age representing 99% of the fish 1) observed, and 2) estimated.

3) Royce's (1972) equation:

$$Z = 4.6/\, t_{max} \tag{6}$$

where: t_{max} is the same as in Hoenig's (1983) estimate above.

4) The slope of a linear regression catch curve (referred to as a "catch curve with equal weighting" in Ricker, 1975, p. 31). In constructing the linear regression catch curve, only Chesapeake Bay fish collected by commercial haul-seine were used, because this gear is considered non-size-selective (Mercer, 1984; Chittenden, 1989). Numbers observed at age were expanded as described above. Data from 1997 and 1998 were pooled in this analysis to minimize the effect of recruitment variability on the mortality estimate (Robson and Chapman, 1961). "t′" was used as described by Beverton and Holt (1956) to be the youngest age fully represented in the catch (where "represented" ≡ "recruited"), and was taken to be one age greater than the age demonstrating the highest log catch (following Pauly, 1984, p. 63). Ages used in the catch curve were truncated 1) on the left, or ascending arm of the catch curve, to t′ and 2) on the right arm of the curve, excluding any age in which 5 or less fish were observed (Chapman and Robson, 1960). The variance and standard error of Z were estimated as variance and standard error of the slope of the regression line.

Analyses in this study were performed both overall and for the individual sexes whenever possible, since differential growth has frequently been reported by sex (Pearson, 1929; Miles, 1950; Guest and Gunter, 1958; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Tabb, 1961; Rutherford, 1982; Mercer 1984; Wenner, 1997) and the fishery cannot distinguish between sexes.

Results

Reproduction

Spotted seatrout have a broad reproductive season – April to August – in the Chesapeake Bay. GSI values and patterns were similar for all study years in both sexes (Fig. 19). Mean GSI values were generally constant and low from late August / early September through early April, indicating little or no spawning throughout that period. GSI values abruptly began to increase in early April, rose to a peak late May / early June, then steadily decreased thru late August / early September.

Chesapeake Bay spotted seatrout show a single annual peak in spawning activity, in late May / early June. In both 1997 and 1998 mean GSI values abruptly rose to a single peak, then rapidly declined through the rest of the summer (Fig. 19). GSI values show little or no evidence of a second major peak in spawning later in the summer.

Macroscopic gonad stages agree with GSI data that spotted seatrout have a broad spawning season in the Chesapeake Bay – April to August. All females collected October through February were in the Regressing/ Resting or Immature Stages, indicating little or no spawning during that period (Fig. 20). Females with Developing Stage ovaries were first seen in March, and more than 70% of the fish were in this stage by April. A small percentage (10 - 20%) of fish continued to enter the Developing Stage from May until September. Fish with

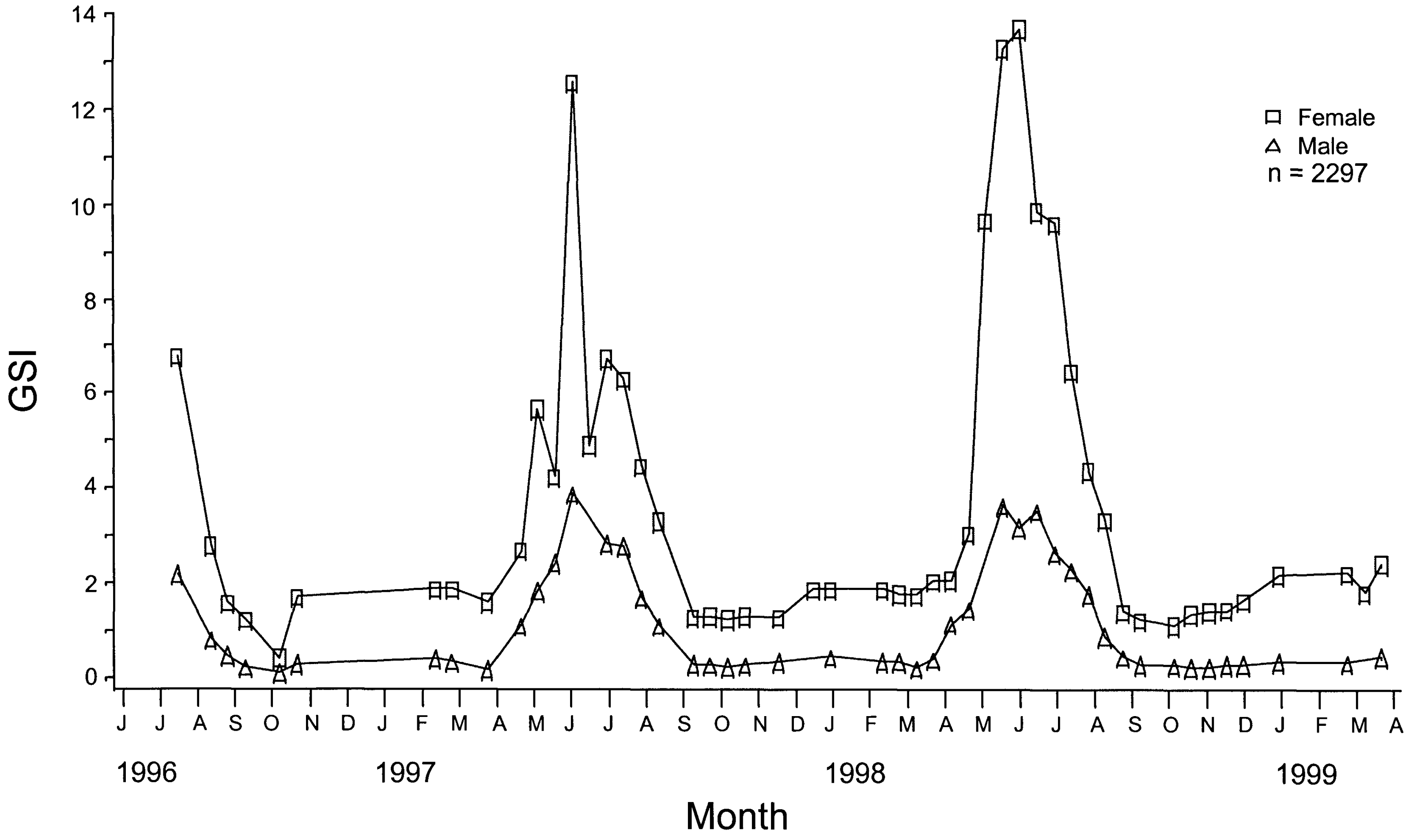


Figure 19. Mean gonadosomatic index (GSI) values for spotted seatrout 1996 - 1999. Data was graphed by fortnight, horizontal axis letters indicate the first day of each month.

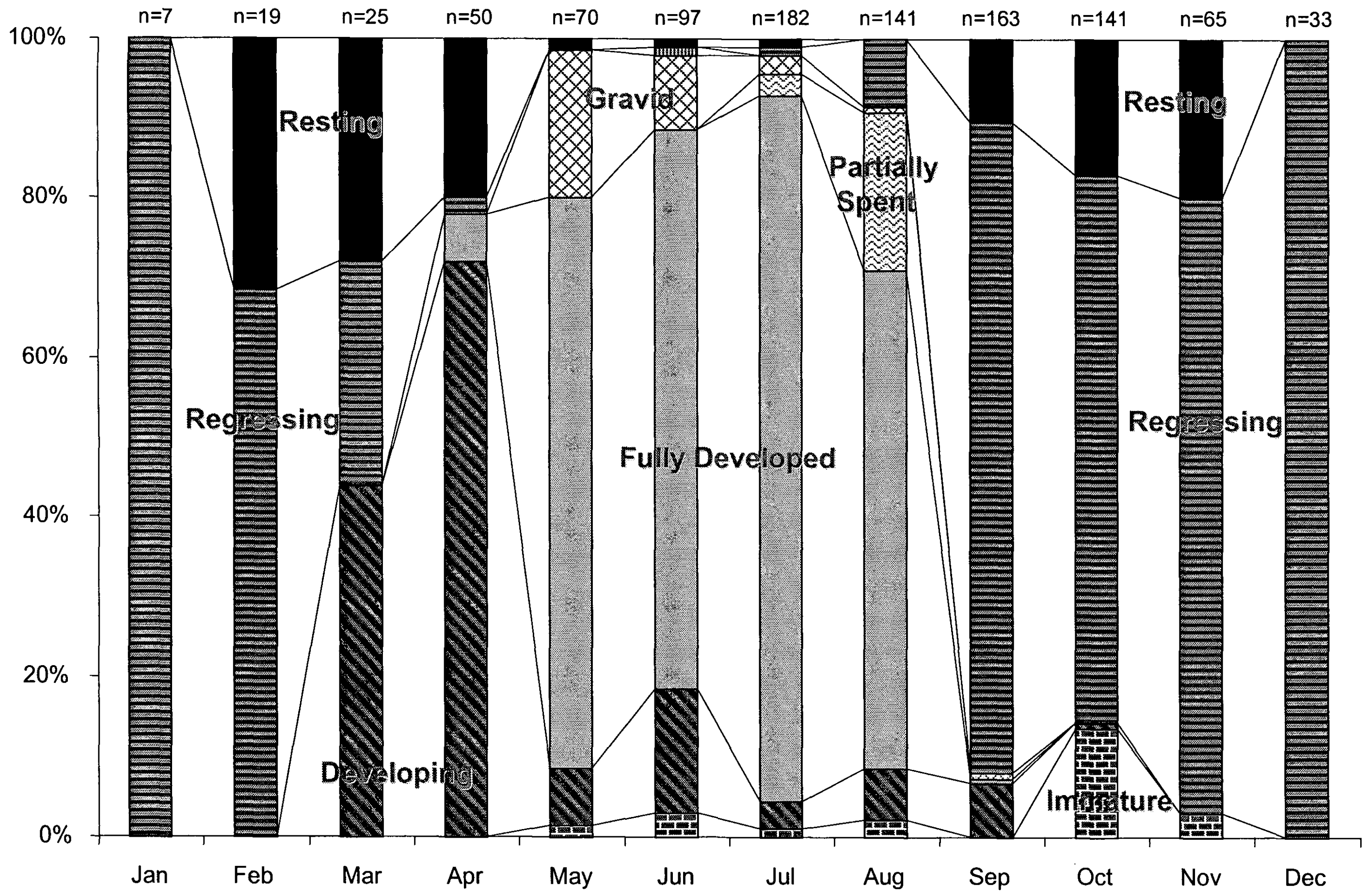


Figure 20. Gonad stage percentages by month for female spotted seatrout. Numbers above each bar indicate the number of ovaries staged that month. Vertical bars in June (not labeled) represent a single Running Ripe fish.

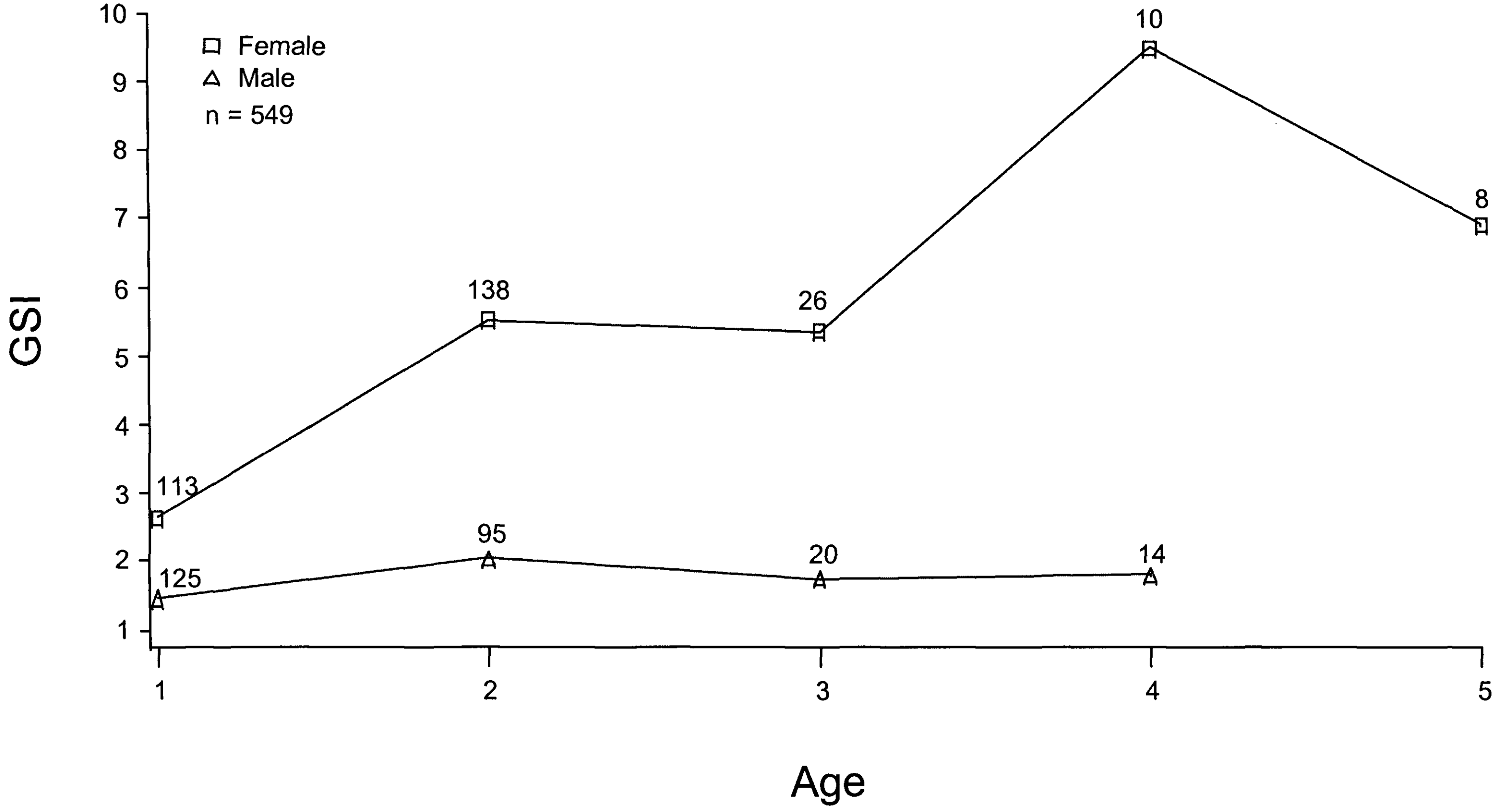


Figure 21. Mean gonadosomatic index (GSI) at age by sex. Numbers at each point indicate the number of observations used to calculate mean GSI. Only those ages with more than 5 observations are included.

Fully Developed Stage ovaries were observed from April until September. Spawning apparently began in May because many fish had Gravid Stage Ovaries then. Gravid ovaries contain hydrated oocytes and indicate imminent spawning. Fish with Gravid Stage ovaries occurred May through August, but were most numerous in May. The only Running Ripe Stage fish was caught on 8 June (Fig. 20), near the peak in GSI values (Fig. 19). Partially Spent Stage fish – which had already spawned – were observed July through August, but they were most common in August.

Spotted seatrout mature at age 1 and 292 mm TL in the Chesapeake Bay. 50 % of female fish were mature at 292 mm. 95% of females were mature by age 1. 100% of female spotted seatrout were mature by 417 mm and age 2. The smallest Fully Mature Stage female was 327 mm, and the youngest observed at this Stage was age 1. The smallest Partially Spent Stage female fish was 358 mm, and the youngest observed at this Stage was also age 1. The smallest Gravid Stage female fish was 353 mm, and the youngest observed at this Stage was age 2. Males appear to be fully mature by age 1, since no significant relationship was observed between male GSI values and increasing age ($P < 0.0537$) (Fig. 21), and male GSI values remained relatively constant for observed ages 1 – 4.

Though female spotted seatrout GSI increases with age, the contribution to spawning may actually decrease at older age. Mean GSI values increased significantly with age for females spotted seatrout ($P < 0.0001$) (Fig. 21) – an indication that female spotted seatrout may contribute more to spawning with age. However, the coefficient of determination ($100r^2$) of this relationship was low at 9.5%, and age 5 fish actually showed lower GSI than age 4 fish. The oldest fish observed, a 10 year old female, was egg-bound – i.e. though this fish's ovarian histology appeared normal and capable of producing eggs, the lumen of each ovary was filled with a waxy substance that blocked eggs from being extruded, thus, this fish was functionally sterile, or "egg-bound." The "waxy" material filling the lumen appeared to be debris from collapsed hydrated ova. The cause of this condition is unknown. In addition, both ovaries of this fish were partially encased in epithelial tissue similar to a granuloma. Though the cause of this condition also remains unknown, it is likely that it was initiated by either a bacterial, fungal, or parasitic infection (D. Zwerner, VIMS, 2000; personal communication).

Age composition

Spotted seatrout were observed to reach a maximum age of at least 10 years and, they are first caught when YOY in the Chesapeake Bay. Overall, 99% (t_{L99}) of spotted seatrout were observed to be 5 years old or less (Table 2), and 99.5% ($t_{L99.5}$) of all fish aged were 6 or less (Table 2A). Expanded age composition, however, indicated $t_{L99.5}$ to be age 5 and less (Table 2B). Observed overall mean age for all fish aged was 2, but mean age for the expanded age composition was 1.3.

Age 1 fish made up the bulk of the catch (Fig. 22). About 40% of all fish actually aged were age 1, 40% were age 2, 12% were age 3, 6% were age 4, 3% were age 5, and less than 1% were older than age 5. Expanded numbers, however, indicated that age 1 fish made up 76%, age 2 made up 21%, age 3 made up 1% and age 4 or older made up less than 2%.

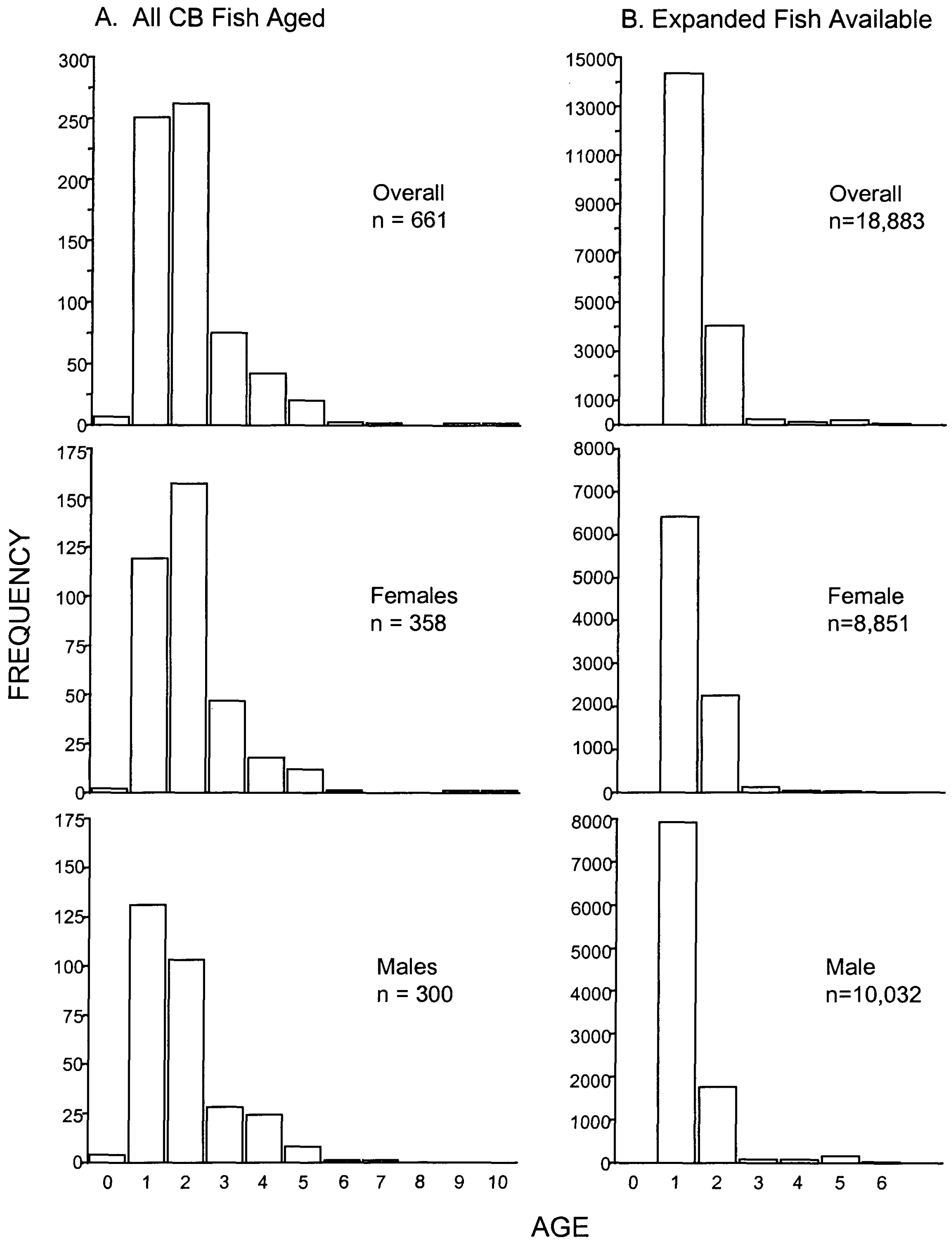


Figure 22. Age composition of all spotted seatrout aged (A) and expanded number of fish available (B). The relative importance of both age 1 fish and males is evident in the expanded age distribution (B), but obscured due to size-stratified subsampling in the raw data (A).

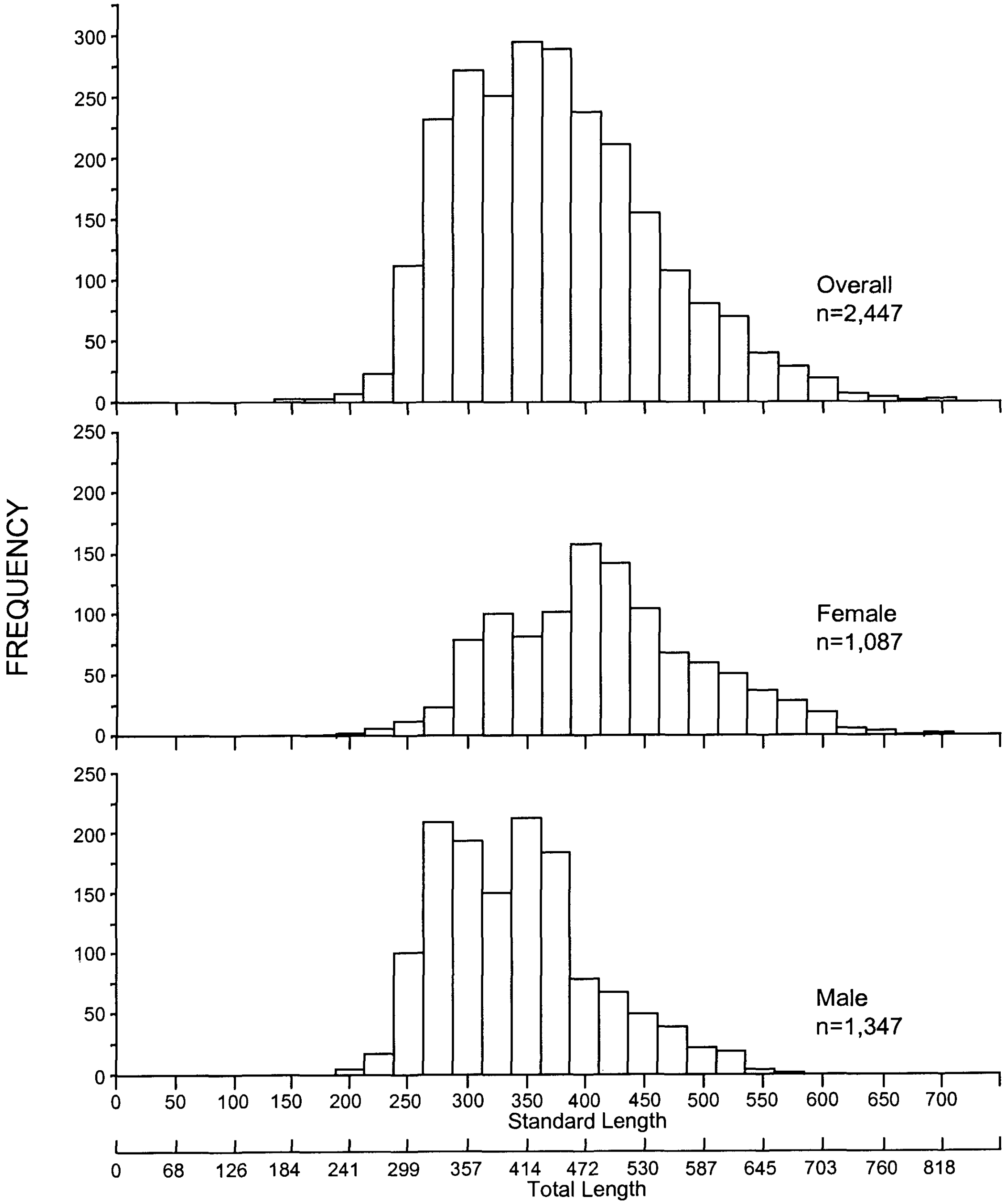


Figure 23. Observed size composition of Chesapeake Bay spotted seatrout.

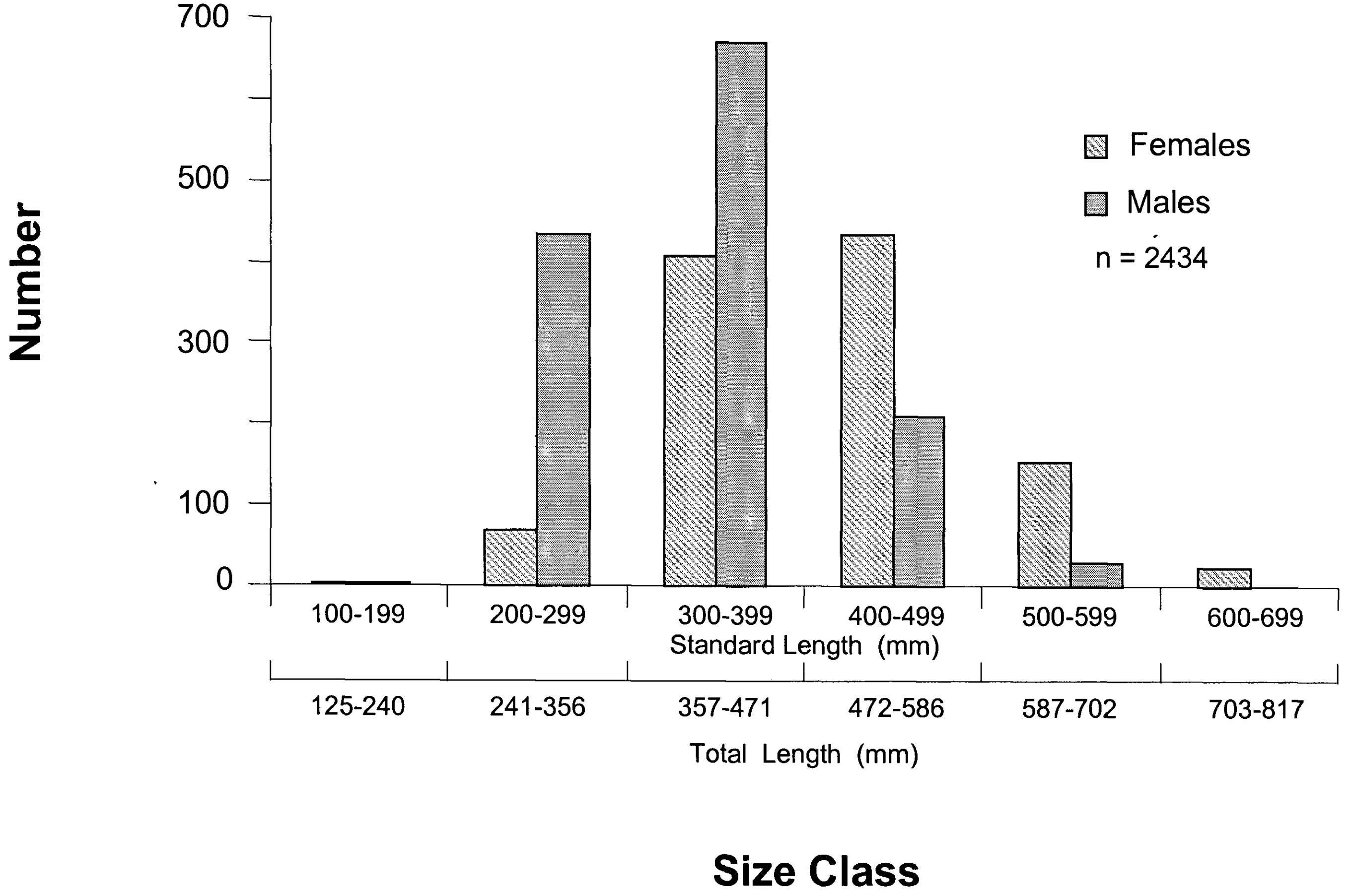


Figure 24. Observed numbers of male and female spotted seatrout, 1996 – 1999 by 100 mm SL size class.

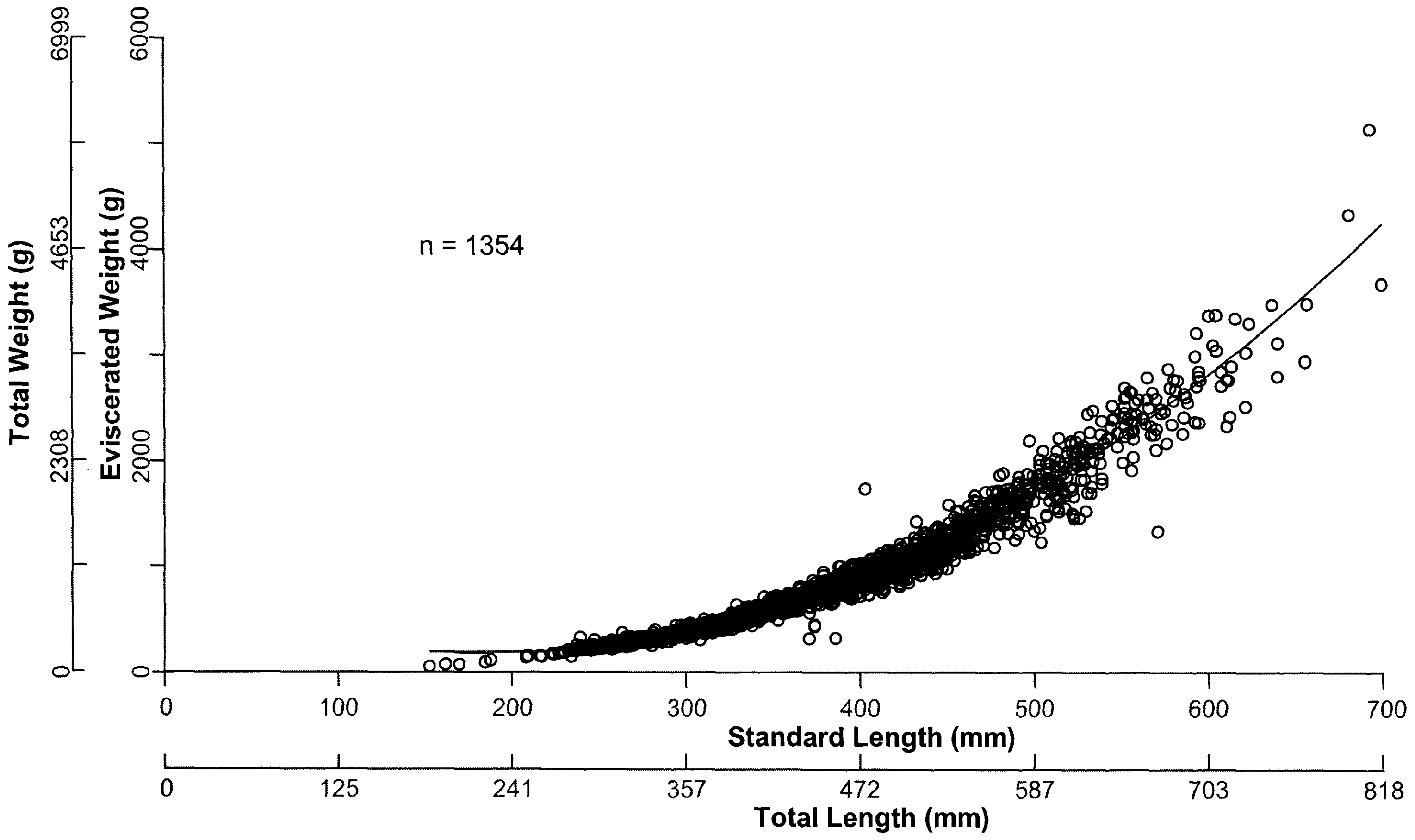


Figure 25. Length - weight relationships for Chesapeake Bay spotted seatrout. The quadratic equation that describes the SL - EW relationship was: $EW = 724.597 - 5.86 * SL + 0.016 * SL^2$.

Maximum observed age was greatest for females (Table 2), but males might actually live longer in the Chesapeake Bay. Observed age at the end of the fishable life span (t_{L99}.) was the same – 5 years – and observed mean age – 1.9 to 2 years – was similar for both sexes. Other than the oldest fish observed – an age 10 female – both observed t_{L99} and $t_{L99.5}$ were the same – ages 5 and 6, respectively – for both sexes. Expanded number at age however, showed that both t_{L99} and $t_{L99.5}$ were greater for males, so males might actually live longer than females in the Chesapeake Bay. Of the 5 fish actually collected age 6 or older, two were male – ages 6 and 7 – and three were female – ages 6, 9 and 10. Mean age differences were significantly different between the sexes ($P > |Z| = 0.0245$, $n = 658$), though that may simply reflect the large sample size (358 female; 300 male).

Age compositions were significantly different among years (1997 and 1998), ($P> |Z| = 0.0001$, $n = 585$). No significant age differences were found between right and left otoliths ($P> |Z| = 0.1809$, $n = 672$).

Size composition

Spotted seatrout were observed to reach a maximum size of at least 817 mm TL, and are first caught at 187 mm in the Chesapeake Bay. Overall, 99.5% ($l_{L99.5}$) of the fish observed were 718 mm or less in length, while 99% (l_{L99}) of spotted seatrout were 696 mm or less. The bulk of the overall catch (66%) was less than 472 mm (Fig. 23). Overall, 90% of the fish were 576 mm or less, 75% were 500 mm or less, and 50% were 432 mm or less in length – a size which corresponds to the peak of the overall size frequency distribution. Mean length overall was 442 mm (Table 3).

Female spotted seatrout grew longer than male fish in the Chesapeake Bay (Fig 24, Table 3). Lengths were significantly different between the sexes ($P> |Z| = .0001$; $n = 2434$), and the observed mean lengths of females – 488 mm – were larger than that of males – 405 mm. Males predominated at sizes below 470 mm TL, but females predominated at larger sizes (Fig. 24).

Length – length, length – girth and log length – log weight relationships are summarized in Table 4. Relationships are presented overall (sexes combined) unless a significant difference was found between the sexes using ANCOVA ($P< 0.0001$). Relationships are presented both overall and by sex when there were significant differences. Previously published length – length and length – weight relationships are given for comparison in Table A1 and A2, respectively. The overall length – weight relationship of Chesapeake Bay spotted seatrout is presented in Fig. 25.

Growth

Chesapeake Bay spotted seatrout grew rapidly until age 4, when growth slowed dramatically. On an overall basis, age 1 spotted seatrout reached a mean length of about 400 mm TL (Table 5). Age 2 and age 3 fish continued to grow quickly – about 100 mm per year. Growth abruptly slowed at age 4, however, so that growth was only about 60 mm/ year between ages 4 – 5, and about 15 mm/ year between ages 5 – 6.

Female spotted seatrout grew more rapidly than males. A 2 year old female was about the same length as a 3 year old male (Table 5). By age 6, the average male still had not reached the average length of a 3 year old female. Size at fractional year age data for all fish combined -- fit to the standard (VBGF) and seasonal (SVBGF) von Bertalanffy growth functions -- also showed that females were larger at age than males (Figs. 26-27). Standard and seasonal von Bertalanffy growth functions fitted to fractional year ages predict asymptotic sizes (L_∞) of 718 – 719 mm overall, 827 – 831 mm for females and 635 – 639 mm for males (Table 6), and k values of 0.46 overall, 0.34 – 0.35 for females and 0.46 – 0.47 for males. Standard VBGF fitted to age from data for a single month -- April, 1998 – predict an asymptotic size (L_∞) of 684 mm and a k of 0.44 (Table 6 - values roughly similar to those of the other von Bertalanffy growth functions; see also Figs. 26 – 28). Estimated growth parameter values were similar in all instances.

Previously published von Bertalanffy parameter values and mean size at age values are presented in Table A3, and Table 8, respectively, for comparison to this study's results.

Mortality

Overall estimates of instantaneous total annual mortality rates (Z) ranged from 0.87 – 1.27. Estimates of Z ranged from 0.88 – 1.59 in females, and between 0.87 – 1.20 in males. The various estimates of Z are presented by method of estimation in Table 7, along with corresponding estimates of survival (S) and total annual mortality (1-S). Table A4 lists Z, S and 1-S values previously published, compared to current results.

Linear regression catch curves, overall and for each sex, are presented in Figure 29. In all instances, catch curves did not depart significantly from linearity.

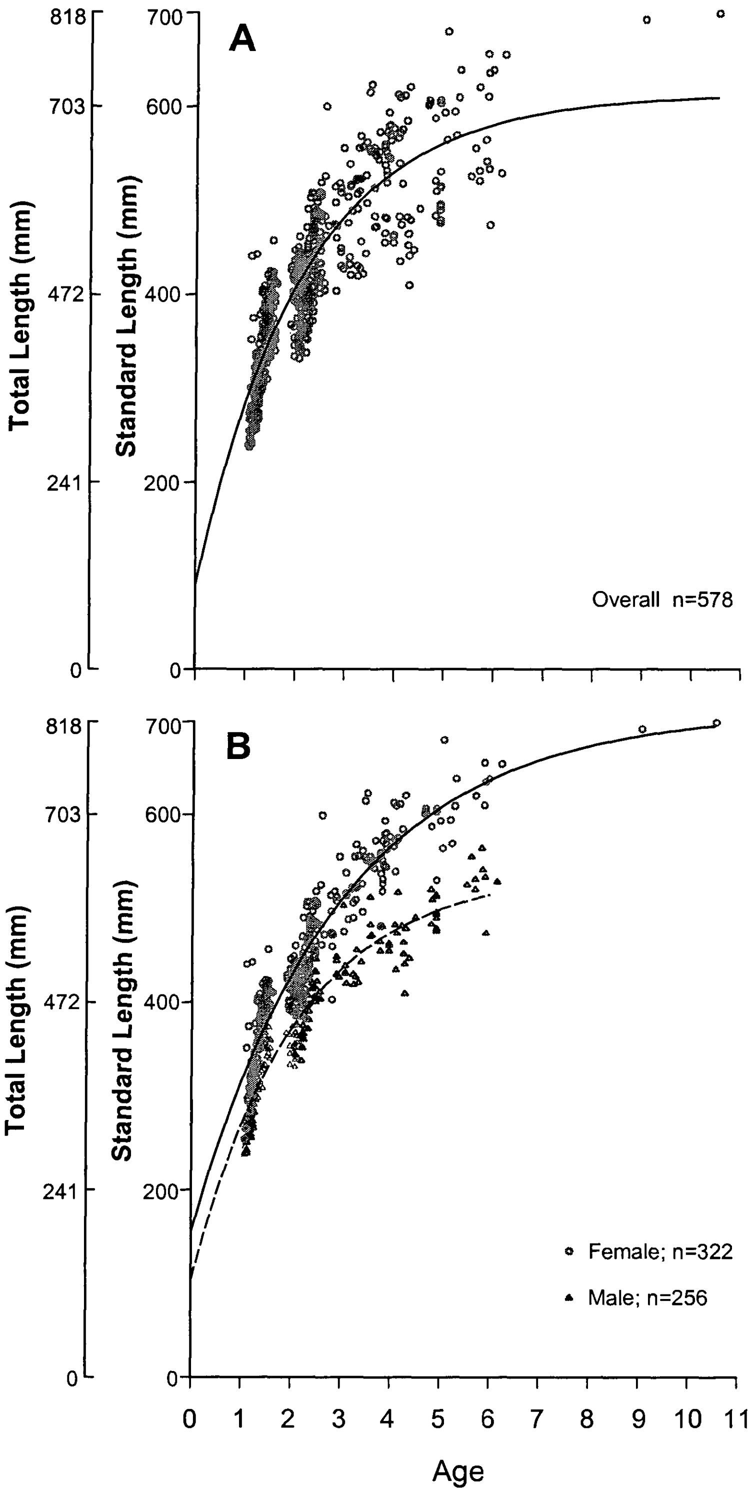


Figure 26. Size at fractional year age data fit to a standard von Bertalanffy growth function (VBGF) for all Chesapeake Bay spotted seatrout pooled (A), and for females and males (B).

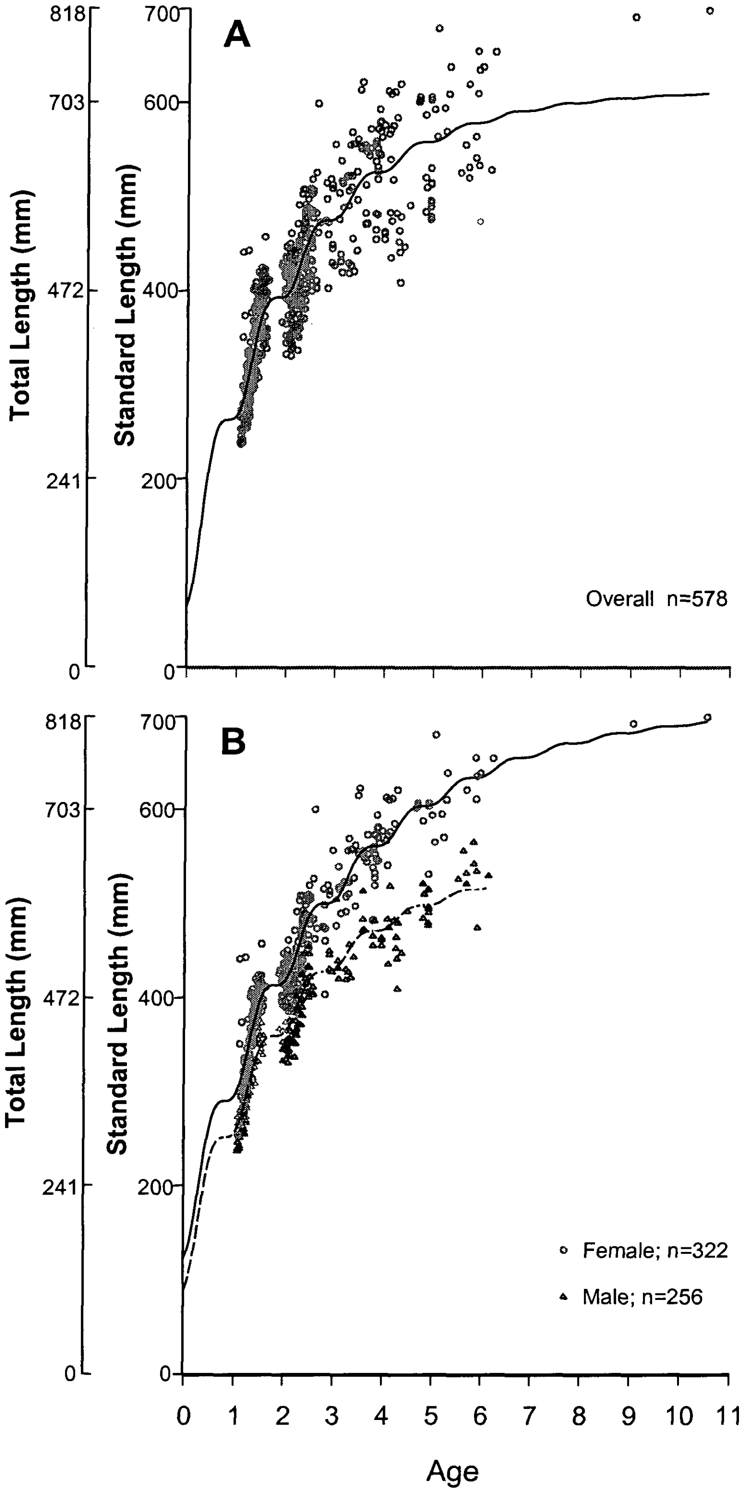


Figure 27. Size at fractional year age data fit to a seasonal von Bertalanffy growth function (SVBGF) for all Chesapeake Bay spotted seatrout pooled (A), and for females and males (B).

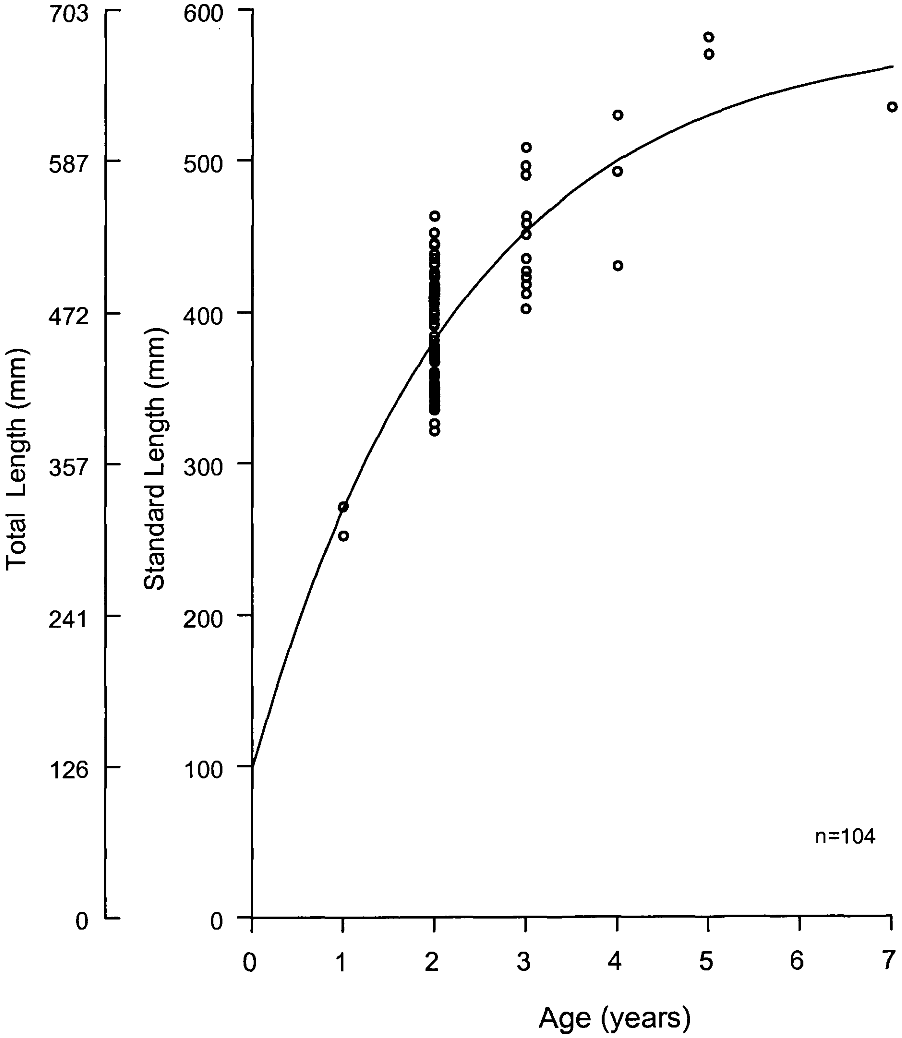


Figure 28. Size at age in years data for all fish collected April 1998 (n = 104), fit to a standard von Bertalanffy growth function.

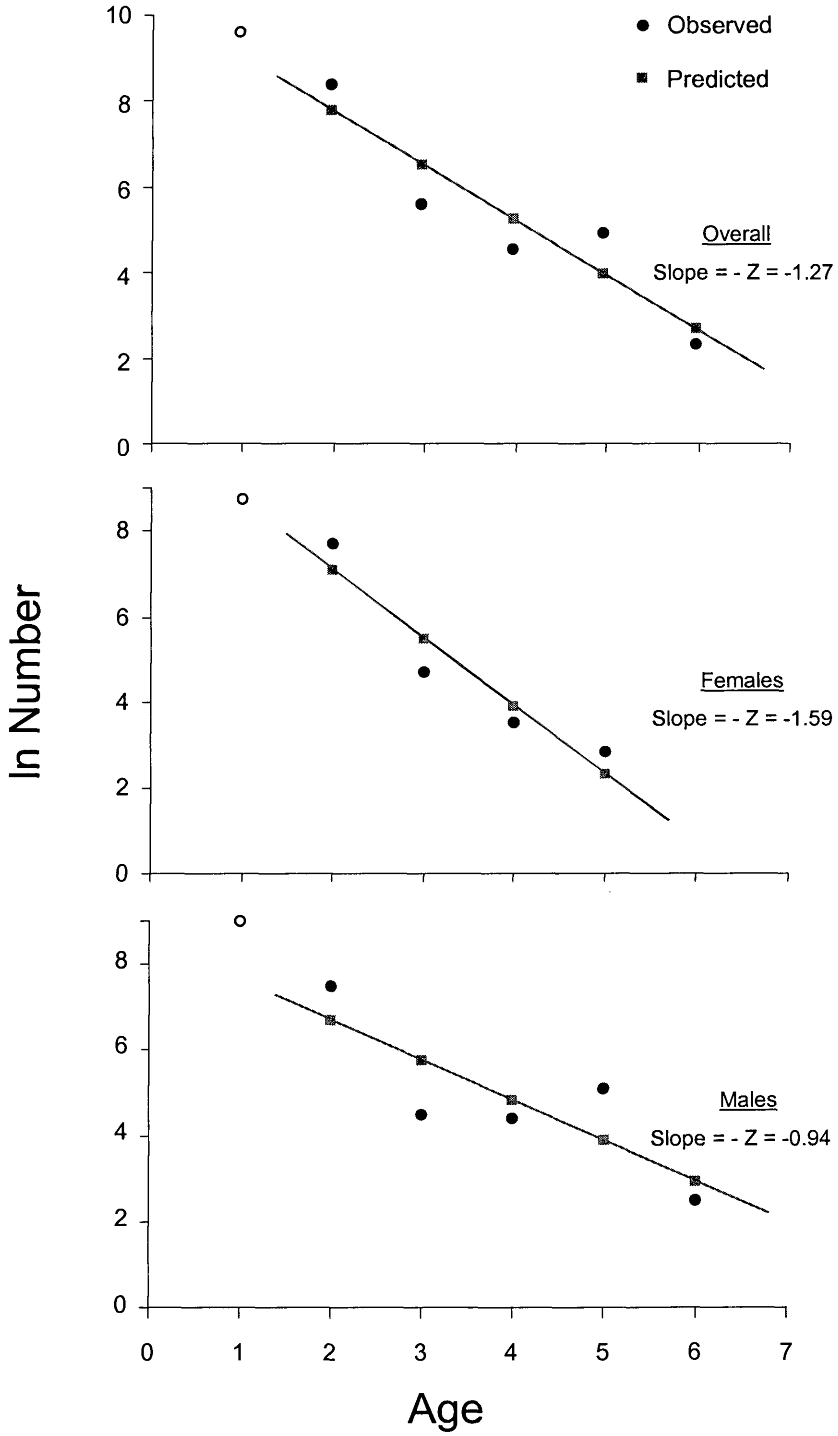


Figure 29. Linear regression catch curves of Chesapeake Bay spotted seatrout. Open circles were not used in estimation of the regression line.

Table 2. Age statistics of spotted seatrout in the Chesapeake Bay, 1996 - 1999.

A. Observed number of fish aged:

		Observed			t_{L99}	$t_{L99.5}$
	n	Min	Max	Mean; SE	99%	99.5%
Overall:	661	0	10	2.0 ; 0.045	5	6
Females:	358	0	10	2.0 ; 0.061	5	9
Males:	300	0	7	1.9 ; 0.065	5	6

B. Based on expanded number of fish at age:

			t_{L99}	$t_{L99.5}$
	n	Mean	99%	99.5%
Overall:	18,883	1.3	5	5
Females:	8,851	1.3	3	4
Males:	10,032	1.3	5	5

Table 3. Observed length statistics of spotted seatrout. All lengths are expressed as TL in mm after converting from SL using my regression of TL on SL.

		Observed			l_{L99}	$l_{L99.5}$
	n	Min	Max	Mean ; SE	99%	99.5%
Overall:	2,447	187	817	442 ; 1.7	696	718
Females:	1,087	207	817	488 ; 2.6	727	748
Males:	1,347	227	662	405 ; 1.8	611	624

Table 4. Length – length, length – girth and length – weight relationships for spotted seatrout collected from the Chesapeake Bay 1996-1999.

Relationship		Equation	SE(slope)	n	r^2
TL – SL	**Overall:**	TL = 10.56 + 1.154 * SL	2.29×10^{-3}	1357	0.995
SL – TL	**Overall:**	SL = -7.00 + 0.862 * TL	1.71×10^{-3}	1357	0.995
G – SL	**Overall:**	G = - 11.63 + 0.627 * SL	3.51×10^{-3}	2245	0.934
	Females:	G = - 11.87 + 0.630 * SL	6.54×10^{-3}	987	0.904
	Males:	G = - 5.95 + 0.607 * SL	4.38×10^{-3}	1258	0.939
SL - G	**Overall:**	SL = 42.09 + 1.49 * G	8.36×10^{-3}	2245	0.934
	Females:	SL = 57.09 + 1.44 * G	1.49×10^{-2}	987	0.904
	Males:	SL = 30.22 + 1.55 * G	1.11×10^{-2}	1258	0.939
$\log_{10}$ EW – $\log_{10}$ SL	**Overall:**	$\log_{10}$ EW = - 4.61 + 2.90 * $\log_{10}$ SL	8.65×10^{-3}	2336	0.980
	Females:	$\log_{10}$ EW = - 4.69 + 2.93 * $\log_{10}$ SL	1.51×10^{-2}	1033	0.973
	Males:	$\log_{10}$ EW = - 4.63 + 2.91 * $\log_{10}$ SL	1.22×10^{-2}	1303	0.978
$\log_{10}$ EW – $\log_{10}$ TL	**Overall:**	$\log_{10}$ EW = - 5.08 + 3.00 * $\log_{10}$ TL	1.08×10^{-2}	1349	0.983
$\log_{10}$ TW – $\log_{10}$ TL	**Overall:**	$\log_{10}$ TW = - 5.26 + 3.09 * $\log_{10}$ TL	1.15×10^{-2}	1349	0.982
	Females:	$\log_{10}$ TW = - 5.22 + 3.07 * $\log_{10}$ TL	2.10×10^{-2}	617	0.972
	Males:	$\log_{10}$ TW = - 5.14 + 3.04 * $\log_{10}$ TL	1.52×10^{-2}	730	0.982

Table 5. Mean size at age of spotted seatrout, observed from all Chesapeake Bay fish aged, 1996 – 1999 (A), and predicted from the standard VBGF fitted to fractional year age (B). SE = standard error of the mean; n = number of observations used in calculating mean. All lengths are TL.

A

Age		Mean Size	SE	n
1	Overall:	402	2.2	251
	Female:	436	4.2	119
	Male:	370	3.4	131
2	Overall:	495	3.0	262
	Female:	525	3.1	157
	Male:	450	3.1	103
3	Overall:	597	6.4	75
	Female:	636	5.1	47
	Male:	532	6.2	28
4	Overall:	619	10.0	42
	Female:	694	7.7	18
	Male:	562	5.8	24
5	Overall:	677	10.8	20
	Female:	713	8.8	12
	Male:	623	9.7	8
6	Overall:	693	63.0	2
	Female:	766	--	1
	Male:	621	--	1

B

Age		Mean Size
1	Overall:	335
	Female:	373
	Male:	319
2	Overall:	479
	Female:	504
	Male:	437
3	Overall:	568
	Female:	599
	Male:	511
4	Overall:	622
	Female:	665
	Male:	557
5	Overall:	654
	Female:	712
	Male:	586
6	Overall:	675
	Female:	747
	Male:	605
7	Overall:	688
	Female:	771
	Male:	616
8	Overall:	696
	Female:	787
	Male:	--
9	Overall:	700
	Female:	800
	Male:	--
10	Overall:	703
	Female:	808
	Male:	--

Table 6. Growth parameter estimates for spotted seatrout of the Chesapeake Bay, arrived at by fitting size at fractional year age data to standard (A) and seasonal (B) von Bertalanffy growth functions, and by fitting April 1998 age data (in years) to a standard VBGF (C). Von Bertalanffy parameter symbols are explained in the text

A	n	L_∞ ; SE	k ; SE	t_0 ; SE
Overall:	578	718 ; 14	0.46 ; $4.0\mathrm{x}10^{-2}$	-0.34 ; $1.0\mathrm{x}10^{-1}$
Female:	322	831 ; 19	0.34 ; $2.9\mathrm{x}10^{-2}$	-0.73 ; $1.1\mathrm{x}10^{-1}$
Male:	256	635 ; 12	0.47 ; $4.3\mathrm{x}10^{-2}$	-0.45 ; $1.1\mathrm{x}10^{-1}$

B	n	L_∞ ; SE	k ; SE	t_0 ; SE	ts ; SE
Overall:	578	719 ; 12	0.46 ; $3.5\mathrm{x}10^{-2}$	-0.38 ; $9.7\mathrm{x}10^{-2}$	0.34 ; $3.7\mathrm{x}10^{-2}$
Female:	322	827 ; 16	0.35 ; $2.6\mathrm{x}10^{-2}$	-0.69 ; $1.1\mathrm{x}10^{-1}$	0.33 ; $3.2\mathrm{x}10^{-2}$
Male:	256	639 ; 10	0.46 ; $3.4\mathrm{x}10^{-2}$	-0.53 ; $9.6\mathrm{x}10^{-2}$	0.33 ; $3.8\mathrm{x}10^{-2}$

C	n	L_∞ ; SE	k ; SE	t_0 ; SE
Overall:	104	684 ; 40	0.44 ; $1.2\mathrm{x}10^{-1}$	-0.42 ; $4.0\mathrm{x}10^{-1}$

Table 7. Estimates of instantaneous total annual mortality rates (Z), survival (S), and total annual mortality (1-S) given by various methods of estimation.

Estimate of: **Method**

Z	**Beverton-Holt**	**Hoenig**	**Royce**	**Catch Curve**
Overall	0.97	0.87	0.92	1.27 ; 3.0×10^{-1} SE
Female	1.26	1.44	1.53	1.59 ; 3.8×10^{-1} SE
Male	0.45	0.87	0.92	0.94 ; 3.7×10^{-1} SE

S	**Beverton-Holt**	**Hoenig**	**Royce**	**Catch Curve**
Overall	0.38	0.42	0.40	0.28 ; 8.4×10^{-2} SE
Female	0.28	0.24	0.22	0.20 ; 7.6×10^{-2} SE
Male	0.64	0.42	0.40	0.39 ; 1.4×10^{-1} SE

1-S	**Beverton-Holt**	**Hoenig**	**Royce**	**Catch Curve**
Overall	0.62	0.58	0.60	0.72 ; 8.4×10^{-2} SE
Female	0.72	0.76	0.78	0.80 ; 7.6×10^{-2} SE
Male	0.36	0.58	0.60	0.61 ; 1.4×10^{-1} SE

Discussion

Reproduction

Spawning periodicity has been well described for spotted seatrout, but most of this information pertains to southern populations. In the Gulf of Mexico, reports generally agree that spawning occurs from late March or early April through September or October (TX: Pearson 1929, Miles 1951, Maceina et al. 1987, Brown-Peterson and Thomas 1988, Colura et al. 1988; LA: Sundararaj and Suttkus, 1962; MS: Overstreet, 1983; Florida: Moody 1950; Klima and Tabb 1959; Stewart 1961). Reports of peak spawning vary greatly, however: in Texas, from April / May (Pearson, 1929; Colura et al., 1988) to June / July (Miles, 1951), and two spawning peaks have even been reported, one peak at the beginning (Maceina et al., 1987) or end (Brown-Peterson and Thomas, 1988) of May, and a second peak in August. In Louisiana, Sundararaj and Suttkus (1962) reported a late spawning peak from July / August while Hein and Shepard (1979) reported two spawning peaks, the first in May and a second that varied between study years from July to August. In Florida, reports also vary widely from late May / early June (Klima and Tabb, 1959; Moffett, 1961) to July (Moody, 1950) to two spawning peaks, a first in May and a second in September (Stewart, 1961).

Much less information on spotted seatrout spawning periodicity has been published for the Atlantic coast, but it is generally reported that the spawning season is at least one month shorter than in the Gulf of Mexico, beginning in April and ending in late July (Tabb, 1961), late August (Brown, 1981; present study) or early September (Wenner, 1997). Most workers have reported that a single spawning peak occurs in May along the Atlantic coast (Mahood, 1975; Wenner, 1997; present study), but Brown (1981) reported two peaks in the Chesapeake Bay. My much larger study found no evidence of the second peak Brown observed in mid-July, so the second peak is probably not important in the Chesapeake Bay.

Most reports indicate that the spotted seatrout is a multiple-spawner, and that individuals spawn repeatedly over days or weeks (Pearson, 1929; Miles, 1951; Guest and Gunter, 1958; Sundararaj and Suttkus, 1962; Overstreet, 1983; Brown-Peterson and Thomas, 1988). Brown-Peterson and Thomas (1988) found no evidence of multiple-spawning in spotted seatrout of the Chesapeake Bay, but my macroscopic staging results suggest repeat spawning probably does occur here, since: Partially Spent fish 1) occurred in July following a drop in the occurrence of Gravid fish and 2) were common in August (about 20% of all observations). Microscopic examination of my spotted seatrout ovaries, however, still needs to be performed to confirm this observation.

Females mature at a larger size in the Chesapeake Bay – 292 mm TL – than in southern waters. Females are reported to reach maturity at lengths between 229 and 253 mm TL in the Gulf of Mexico (Moody, 1950; Klima and Tabb, 1959; Stewart, 1961; Overstreet, 1983). Along the Atlantic Coast, in South Carolina, Wenner (1997) also reported size at first maturity to be 254 mm.

In the Chesapeake Bay, however, both Brown (1981) and my study observed a size at first maturity – 290 to 350 mm – that was 40 - 60 mm longer than in the south.

My finding – that females are first mature at age 1 – agree with most published reports that minimum age at first maturity is age 1 for females (Pearson, 1929; Moody, 1950; Klima and Tabb, 1959; Stewart, 1961; Sundararaj and Suttkus, 1962; Colura et al. 1988; present study). Brown (1981), however, reported that her minimum size at maturity corresponded to age 2 fish.

Sundararaj and Suttkus (1962) and Overstreet (1983) both reported increased egg production with increased length of Gulf of Mexico spotted seatrout. Accordingly, both studies indicated that age 2 spotted seatrout are much more important for spawning than are age 1 fish. Sundararaj and Suttkus (1962) point out, however, that a cohort has decreasing "spawning power" with increased age because less fish survive to spawn with increasing age. My results seem to support this idea. Though mean GSI did increase with increased age for Chesapeake Bay females, this relationship was weak, and the oldest fish collected had multiple diseases that prevented spawning.

Age composition

My maximum age of 10 agrees closely with the results of most previous authors (Pearson – 9, 1929; Klima and Tabb – 7, 1959; Moffett – 8, 1961; Tabb – 10, 1961; Stewart – 7, 1961; Maceina et al.– 12, 1987; Rutherford et al. – 8, 1989b; Murphy and Taylor – 9; 1994). Though Brown (1981) claimed that maximum age was 15+ for Chesapeake Bay spotted seatrout, my results indicate that this is unlikely, since 1) Brown's scale-based ages are highly questionable in this region (see Chapter 2), and 2) her age "15" fish (assumed to be female) was only 776 mm TL , which corresponds to an age 7 fish in my much larger study of the same population. Assuming Brown's age "15" fish was overaged, there does not appear to be a difference in maximum age between northern and southern populations of spotted seatrout.

The age distribution of my collection – ages 0 to 10, but dominated by age 1 – was younger than has been reported previously for spotted seatrout. Published figures vary, and have indicated the catch to be dominated by: ages 1 – 4 (Pearson, 1929); ages 1 - 3 (Klima and Tabb, 1959; Moffett, 1961); ages 2 – 3 (Stewart, 1961); age 3 (Tabb, 1961) and ages 3 – 4 (Rutherford, 1982). Of these studies however, only Pearson's was based on non-selective haul seine collections. The others were based on hook and line collections from the sport fishery, (or a combination of hook and line with another gear), and were likely subject to gear selectivity for older ages.

The differential survival by sex that I found in spotted seatrout – 20-28% in females; 39-64% in males – has been noted by many authors (Klima and Tabb, 1959; Tabb, 1961; Rutherford, 1982; Mercer, 1984; Wakeman and Ramsey, 1985; Murphy and Taylor, 1994), however, only Murphy and Taylor (1994) in Florida reported results similar to mine where survival was greatest for males (46-52%), rather than females (29-33%). The oldest spotted seatrout ever recorded was male, age 12 and 637 mm TL (Maceina et al., 1987).

Size composition

The maximum size observed in this study – 817 mm TL – falls in the range of previously published values (all are mm TL): Moody – 563 (1950); Moffett – 660 (1961); Mahood – 633 (1975); Harrington et al.– 902 (1979); Overstreet – 625 (1983); Maceina et al. – 726 (1987); Murphy and Taylor – 806 (1994). Maximum size does not appear to be related to latitude since the largest 3 fish were from extremes of the spotted seatrout range in the U.S., Texas, Virginia and Florida. The peak of my size frequency distribution – about 440 mm – was roughly 130 mm greater in length than those peaks previously published, which ranged from 240 – 364 mm TL (Klima and Tabb, 1959; Moffett, 1961; Rutherford, 1982). Mean length in my study – 442 mm overall; 488 in females; 405 in males – was also longer than those previously reported: Moody – 321 (1950), Rutherford – 386 (1982). The greater peak and mean lengths reported here were likely results of faster growth in the Chesapeake Bay, as described below.

I found that female spotted seatrout grow longer than males. Differential growth by sex that I observed in the Chesapeake Bay is consistent with reports throughout the range of the spotted seatrout (Pearson, 1929; Moody, 1950; Miles, 1951; Guest and Gunter, 1958; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Tabb, 1961; Iversen and Tabb, 1962; Brown, 1981; Rutherford, 1982; Overstreet, 1983; Colura et al., 1984; Maceina et al., 1987; Murphy and Taylor, 1994; Wenner, 1997).

My length – length relationships were similar to length – length relationships for spotted seatrout previously described for Texas (Harrington et al., 1979; Maceina et al., 1987), Mississippi (Overstreet, 1983) and Florida (Moffett, 1961; Murphy and Taylor, 1994). Because these relationships are all so similar, it appears this morphometric relationship is fairly constant between populations.

The coefficients of my log length – log weight relationships for spotted seatrout of the Chesapeake Bay – a = -4.75 to -5.26; b = 2.97 to 3.09 (see Table A2) – appeared to correspond well to those reported from West Florida (Moffett, 1961; Murphy and Taylor, 1994), South Florida (Rutherford, 1982), Mississippi (Overstreet, 1983), and to Louisiana and Texas (Wakeman and Ramsey, 1985) (Table A2). In spite of this, my relationship poorly predicted weight for estuaries other than the Chesapeake Bay. Thus, when using a length – weight relationship, it is advisable to use one specific to the estuary of concern. My length – weight data do not support Brown's (1981) hypothesis that Chesapeake Bay fish are heavier at given length than fish of other areas. When Brown put forth this idea, she also pointed out that the weight difference between Chesapeake Bay fish and fish of other areas could have been due to sampling time bias in her data, since her collection occurred only in summer, when feeding was heavy and gonads were large. The latter was likely the case, since my weights were significantly lower at length than Brown's, and unlike Brown's weights; mine were based on year-round collection.

Growth

Spotted seatrout are larger at any given age in the Chesapeake Bay than they are in more southern populations. The growth rates I observed in the Chesapeake Bay are by far the greatest ever reported for this species (Figs. A2 and A3). The mean length of 1 year old Chesapeake Bay fish overall (402 mm) was about 150 mm longer than the combined average reported values of Florida (Tabb, 1961; Rutherford, 1982) and Louisiana (Wakeman and Ramsey, 1985) (see Table 7 for reported mean lengths at age from each study). Mean length of age 1 Chesapeake Bay females (436 mm) was about 50 mm longer, and mean length of age 1 males (370 mm) was about 20 mm longer than the combined average lengths in Florida (Murphy and Taylor, 1994) and Texas (Maceina et al., 1987). By age 3, my fish were about 225 mm longer overall (597 mm) than the same age fish in Florida (Tabb, 1961; Rutherford, 1982) or Louisiana (Wakeman and Ramsey, 1985), and both female and male Chesapeake Bay fish (636 and 532, respectively) were about 125 mm longer than their counterparts in Florida (Murphy and Taylor, 1994; Rutherford, 1982) or Texas (Maceina et al., 1987). By age 5, my fish overall (677mm), were still about 140 mm longer than fish in Florida (Tabb, 1961; Rutherford, 1982) or Louisiana (Wakeman and Ramsey, 1985), while age 5 females (713 mm) were 100 mm longer, and males (623 mm) were 130 mm longer in Chesapeake Bay than in Florida (Murphy and Taylor, 1994; Rutherford, 1982) or Texas (Maceina et al., 1987).

Observed mean size at age from this study were compared only to previous studies that reported observed mean size at age. Those studies which used backcalculation techniques to determine mean size at age (Pearson, 1929; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Brown, 1981; Rutherford, 1982; Colura et al., 1984; Maceina et al., 1987), generally reported much slower growth rates than those studies that reported observed mean size at age, even though the geographic range of study sites were similar (Chesapeake Bay, south Florida, west Florida, northwest Florida and Texas). The depressed growth rates reported in backcalculation studies were probably a consequence of Lee's phenomenon, where backcalculated size at a given age tends to be smaller than observed size at the same age (Ricker, 1975). Mean size at age predicted from the VBGF lags behind observed values, because the von Bertalanffy equation predicts length of the fish at the time of mark formation, which occurs early in the spring here, before most of the year's growth takes place.

Data fit separately with the standard VBGF and the SVBGF yielded the same parameter estimates. Although the seasonal curve tracked the data well, the SE decreased by only 8% compared to the standard VBGF. I used the standard VBGF to compare my growth parameter values with previously published reports because parameter estimates differed little and the standard VBGF is used in most previously published reports. My fit of age data from April 1998 produced parameter estimates similar to those from the standard VBGF and the SVBGF based on fractional year age, but the parameter estimates were much more variable for April 1998, in part because the fit was based on fewer observations.

Table 8. Observed mean size at age for spotted seatrout from various locations. Lengths in Tabb (1961), Rutherford (1982), Wakeman and Ramsey (1985) and Maceina et al. (1987) were converted from SL to TL using Murphy and Taylor's observed relationship in 4,884 Florida spotted seatrout: TL = 10.26 = 1.1399 * SL

		Mean TL (mm) at Age						
Study Site	Author(s)	1	2	3	4	5	6	7
Chesapeake Bay	Present study							
	Overall:	402	495	597	619	677	693	--
	Females:	436	525	636	694	713	766	--
	Males:	370	450	532	562	623	621	--
E. Florida	Murphy & Taylor							
	(1994) Females:	401	501	576	651	728	728	750
	Males:	355	394	439	482	506	564	621
W. Florida	Females:	364	435	510	551	573	617	642
	Males:	324	351	384	421	437	485	512
N.W. Florida	Females:	381	477	546	650	699	684	--
	Males:	326	381	413	449	522	--	--
E. Florida	Tabb (1961)*	276	325	419	504	593	626	667
S. Florida	Rutherford*							
	(1982) Overall:	276	332	368	419	484	489	586
	Females:	280	329	376	431	497	490	586
	Males:	274	333	358	398	459	483	--
Louisiana	Wakeman & Ramsey (1985)*	193	272	352	421	--	--	--
Texas	Maceina et al. *							
	(1987) Females:	389	444	541	609	638	666	672
	Males:	357	406	463	492	510	524	497

The VBGF fit size at age data well in this study. There was a wide range in size data and asymptotes were well described overall and for both males and females. My "overall" L_∞ value – 718 – falls in the lower range of the previously reported L_∞ values (Chesapeake Bay: Brown – 935 (1981); S. FL: Rutherford – 893 (1982), Louisiana: Wakeman and Ramsey – 708 (1985); Gulf of Mexico: Condrey et al. – 655 (1985)). The largest overall estimates (Brown, 1981; and Rutherford, 1982) appear to be inflated, since 1) the overall L_∞ values in these studies were much greater than either the female or the male L_∞ estimates, and 2) neither the Brown nor the Rutherford study had well-described asymptotes. Overestimating L_∞ is a common problem when data do not clearly suggest an asymptote (M. Chittenden, 1999; personal communication). Also, Chittenden points out, when L_∞ is overestimated, k will be underestimated. Probably because of this, both Brown's (1981) and Rutherford's (1982) overall k estimates were exceedingly small – an order of magnitude lower than other k estimates. My female L_∞ estimate – 831 – was in the upper range of previous estimates (Chesapeake Bay: Brown – 854 (1981); Florida: Murphy and Taylor: E. FL – 839, W. FL – 698, N.W. FL – 818 (1994); S. FL: Rutherford – 768 (1982); Texas: Colura et al. – 525 (1984); Maceina et al. – 687 (1987)), and my male L_∞ estimate – 635 – falls in the middle of previous estimates (Chesapeake Bay: Brown – 760 (1981); S. FL: Rutherford – 684 (1982); Texas: Colura et al. – 487 (1984); Maceina et al. – 664 (1987)).

Differences between studies in L_∞, and k estimates do not appear attributable to latitude or differences between the Gulf of Mexico and Atlantic, since my overall estimates were most similar to those presented by Wakeman and Ramsey (1985) in Louisiana, and my female estimates were most comparable to Murphy and Taylor's (1994) from east and northwest Florida.

Mortality

The range of estimates for the overall instantaneous rate of total annual mortality (Z) varied little between the four different estimation methods in this study. Overall Z values were highest for the linear regression catch curve (CC) estimate, while the Beverton-Holt (1956) (BH) and maximum age estimators of Hoenig (1983) (H) and Royce (1972) (R) all predicted similar Z values. However, none of the differences were great between overall estimates, and the corresponding survival "S" estimates differed little between the high (.42) and low (.28) values.

The four Z estimators also produced similar results when mortality and survival were examined by sex. Female estimates of Z ranged between 1.26 and 1.59, and corresponding S estimates differed very little between the high (.28) and low (.20) values. Male estimates of Z varied more and ranged between 0.45 and 0.94, however, these differences were not great, and corresponding S estimates varied moderately between the high (.64) and low (.39) values. All four estimators indicated a higher mortality for females.

Other data also seem to indicate that mortality is higher for females in the Chesapeake Bay: 1) more males (55%) were observed in the catch than females

(45%); 2) t_{L99} and $t_{L99.5}$ values were greater for males (by 2 years and 1 year, respectively) when numbers at age were expanded, indicating males have a greater survival than females. This observation is likely a result of the fishery rather than the biology of the animal, however. Since female spotted seatrout were observed to grow faster than males in the Chesapeake Bay, it is likely that more females are caught earlier in life, and consequently suffer higher mortality than males.

My overall Z estimates – 0.87 to 1.27 – were generally in the middle of the range of estimates reported previously throughout the range of spotted seatrout (Table A4). Of those that reported overall estimates of Z -- South Carolina: Wenner – 0.70 (1997); S. Florida: Stewart – 1.28 (1961); Rutherford – 1.47 (1982); Rutherford – 0.43–1.0 (1989b); W. Florida: Iversen and Moffett - .447 (1962); Louisiana: Wakeman and Ramsey – 1.139 (1985); Texas: Baker et al. – 1.13-1.57 (1986) -- Rutherford's 1982 estimate exceeded my estimated range, Baker's (1986) range overlapped and exceeded mine, but Rutherford's 1989(b) estimates (a larger study from the same region studied in 1982) overlapped mine at the low end of my range, and Iversen and Moffett's (1962) value was lower than my range entirely. Wenner (1997), Stewart (1961), and Wakeman and Ramsey (1985) all presented estimates similar to my own.

My Z estimates for each sex – 1.26 to 1.59 for females; 0.45 to 0.94 for males – were generally similar to those reported in: Florida: Murphy and Taylor – females: 1.11-1.24 – males: 0.65-0.78 (1994), and Louisiana: Wakeman and Ramsey – females: 1.02 – males: 1.83.(1985). However, female estimates from these studies were slightly lower than those presented here, and though Murphy and Taylor's (1994) male estimate corresponded closely to mine, Wakeman and Ramsey's (1985) male estimate was more than twice the Z observed here.

When mortality differs by sex and the fishery cannot distinguish between the sexes -- like for spotted seatrout -- it is best to use the estimate for the sex with the lowest mortality rate for yield modeling, in this study the male estimate. If the high estimate, or an overall estimate is used instead, mortality would be overestimated for one sex and that would overestimate that sex's ability to withstand fishing pressure.

Appendix. Results of previously published spotted seatrout studies compared with those presented here for spotted seatrout of the Chesapeake Bay.

Study Site	Author(s)	a	b	Calculated TL of a 200mm SL fish	Calculated TL of a 700mm SL fish	n
Chesapeake Bay	Present study	10.56	1.154	241	818	1,357
Florida	Murphy and Taylor (1994)	10.26	1.1399	238	808	4,884
W. Florida	Moffett (1961)	0	1.22	244	854	307
Mississippi	Overstreet (1983)					
	Females:	10.6586	1.1284	236	801	1,680
	Males:	10.1648	1.1292	236	801	1,089
Texas	Harrington et al. (1979)	11.804	1.138	239	808	9,857
Texas	Maceina et al. (1987)	12.41	1.411	295	1000	444

Table A1. Previously published total length – standard length relationships for spotted seatrout compared with the overall TL – SL relationship in the present study. Relationships are presented as the linear equation: TL = a + b * SL, where "a" is the y-axis (TL) intercept, and b is the slope of the line. "n" is the number of fish that each relationship was based on.

Table A2. Previously published length – weight relationships for spotted seatrout are compared to those of the present study. All relationships are presented as: $\log_{10}$ weight = $\log_{10}$ a + b * $\log_{10}$ length ;where "a" is the y-axis (TL) intercept as in legend of Table A1. I assumed that Moffett's (1961) relationship was in mm, not cm, as stated in his caption.

Study Site	Author(s)	Specific length-weight relationship	a	b	Predicted weight (g) for 200 mm length fish	Predicted weight (g) for 700 mm length fish	n
Chesapeake Bay	Present study	logTW-logTL	-5.26	3.09	70.8	3399.0	1,349
Chesapeake Bay	Brown (1981)	“	-5.072	3.043	85.1	3851.5	176
W. Florida	Moffett (1961)**		-5.3333	3.1131	67.6	3340.2	307
Chesapeake Bay	Present study	logEW-logTL	-5.08	3.00	66.5	2852.9	1,349
E. Florida	Murphy & Taylor						
	(1994) Female:	“	-5.3822	3.1174	61.8	3069.8	1,444
	Male:		-5.4536	3.1500	62.3	3224.5	675
W. Florida	Female:		-5.0725	2.9946	65.8	2801.8	2,899
	Male:		-5.2728	3.0788	64.8	3066.8	1,394
N.W. Florida	Female:		-5.3278	3.0886	60.1	2881.2	787
	Male:		-5.7841	3.2655	53.7	3210.5	376
Chesapeake Bay	Present study	logTW-logSL	-4.75	2.97	124.8	5177.9	2,430
S. Florida	Rutherford (1982)	“	-5.1912	2.7450	133.4	4155.0	567
			(decagrams)				
Mississippi	Overstreet (1983)						
	Female:		-4.9472	3.0516	118.7	5431.3	1,683
	Male:		-4.9466	3.0510	118.5	5417.4	1,087
Louisiana	Wakeman & Ramsey		-1.6664	2.8996	127.7	4826.7	561
	(1985)		(length in cm)				
Texas			-1.5719	2.8204	125.2	4285.6	54

Study Site	Author(s)		L_∞	k	t_o
Chesapeake Bay	Present study				
		Overall:	718	0.46	-0.34
		Female:	831	0.34	-0.73
		Male:	635	0.47	-0.45
Chesapeake Bay	Brown (1981)				
		Overall:	935	0.059	-5.6091
		Female:	854	0.052	-7.9278
		Male:	760	0.052	-7.5933
E. Florida	Murphy & Taylor (1994)				
		Female:	839.2	0.3617	0.74
		Male:	*	*	*
W. Florida		Female:	698.3	0.3633	0.39
N.W. Florida		Female:	817.7	0.3496	0.68
S. Florida	Rutherford (1982)**				
		Overall:	893	0.09	-2.54
		Female:	768	0.13	-2.04
		Male:	684	0.12	-2.95
Louisiana	Wakeman & Ramsey‡ (1985)		708	0.3364	(0) Assumed
Texas	Maceina et al. (1987)				
		Female:	687.0	0.512	0.260
		Male:	663.5	0.179	1.939
Texas	Colura et al. (1984)				
		Female:	524.8	0.42	-0.07
		Male:	486.8	0.33	-0.08
Gulf of Mexico	Condrey et al. (1985)		655	0.2005	-0.4113

* Murphy & Taylor reported linear growth for males in all Florida study sites

** Measurements converted from SL to TL using Murphy & Taylor's reported relationship for Florida:
TL = 10.26 + 1.1399 * SL

‡ Measurements converted from SL to TL using Harrington's reported relationship for Texas:
TL = 11.804 + 1.138 * SL

Table A3. Von Bertalanffy parameter estimates compared to previous reports.

Study Site	Author(s)		Z	S	1-S
Chesapeake Bay	Present study	Overall:	0.87 - 1.27	0.28 - 0.42	0.58 - 0.72
		Female:	1.26 - 1.59	0.20 - 0.28	0.72 - 0.80
		Male:	0.45 - 0.94	0.39 - 0.64	0.36 - 0.61
South Carolina	Wenner, (1997)		1.205	0.30	0.70
Florida	Murphy and Taylor (1994)				
		Female:	1.11-1.24	0.29 - 0.33	0.67-0.71
		Male:	0.65-0.78	0.46 - 0.52	0.48-0.54
S. Florida	Stewart (1961, raw data only; *reported in* Rutherford,1982)		1.28	0.28	0.72
S. Florida	Rutherford (1982)		1.47	0.23	0.77
S. Florida	Rutherford (1989b)		0.43-1.0	0.37 - 0.65	0.35-0.63
W. Florida	Iversen and Moffett (1962)		0.447	0.64	0.36
Louisiana	Wakeman and Ramsey (1985)	Overall:	1.139	0.32	0.68
		Female:	1.02	0.36	0.64
		Male:	1.83	0.16	0.84
Texas	Baker et al. (1986)		1.13-1.57	0.20-0.32	0.67-0.80

Table A4. Summary of published total annual mortality and survival estimates for spotted seatrout.

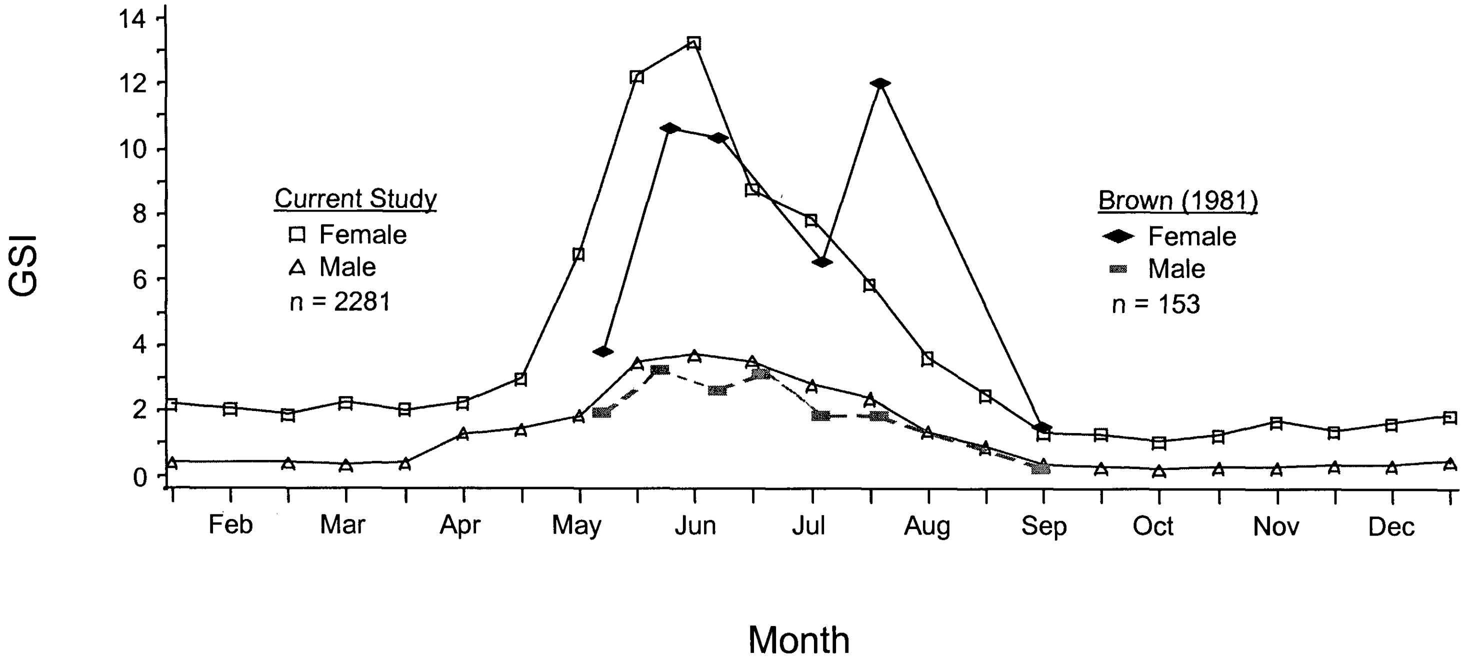


Figure A1. Peak spawning for spotted seatrout in the Chesapeake Bay, 1996 – 1999 (current study) and 1979 – 1980 (Brown, 1981).

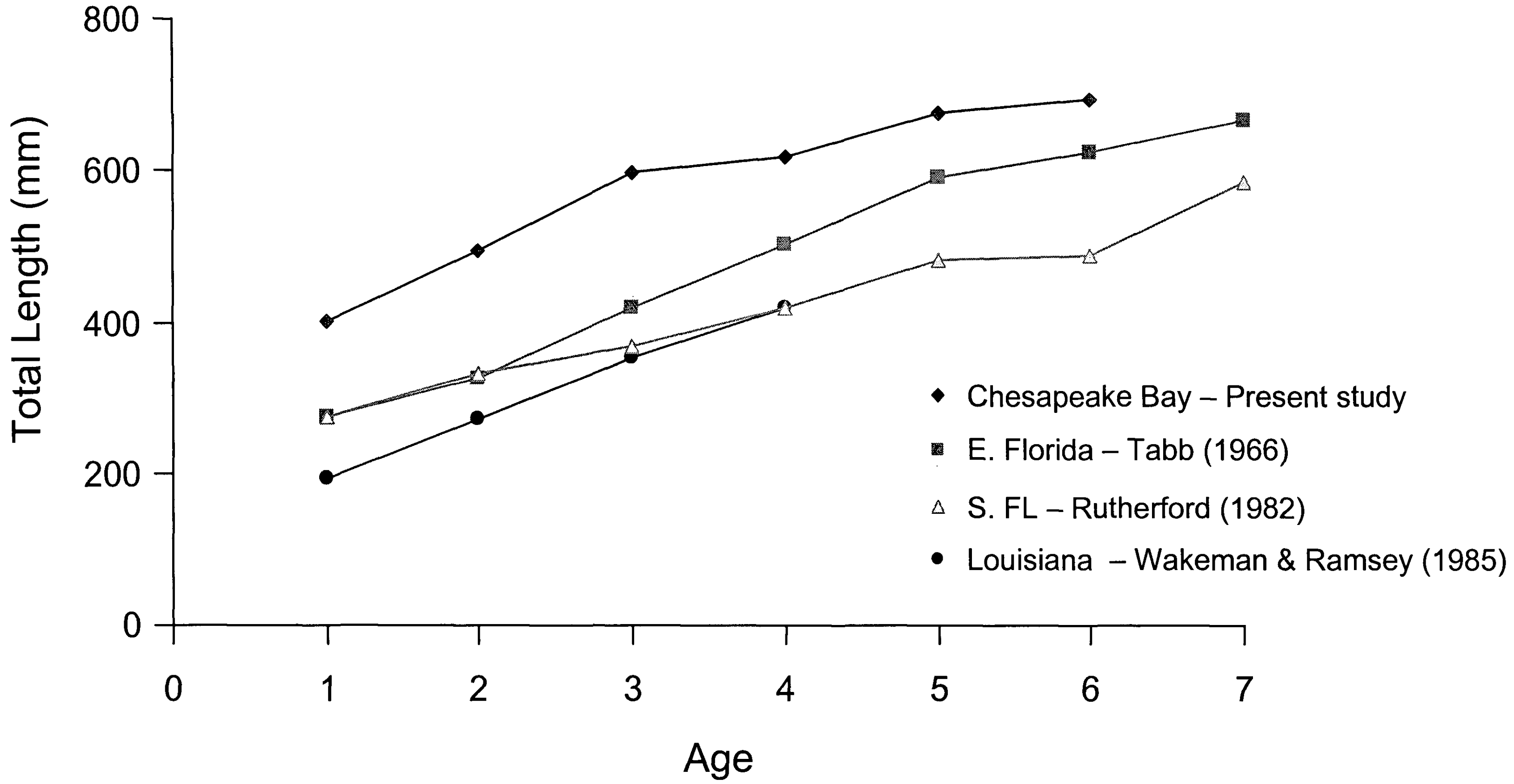


Figure A2. Previously published observed mean size at age for spotted seatrout, compared with the observed mean size at age in the present study.

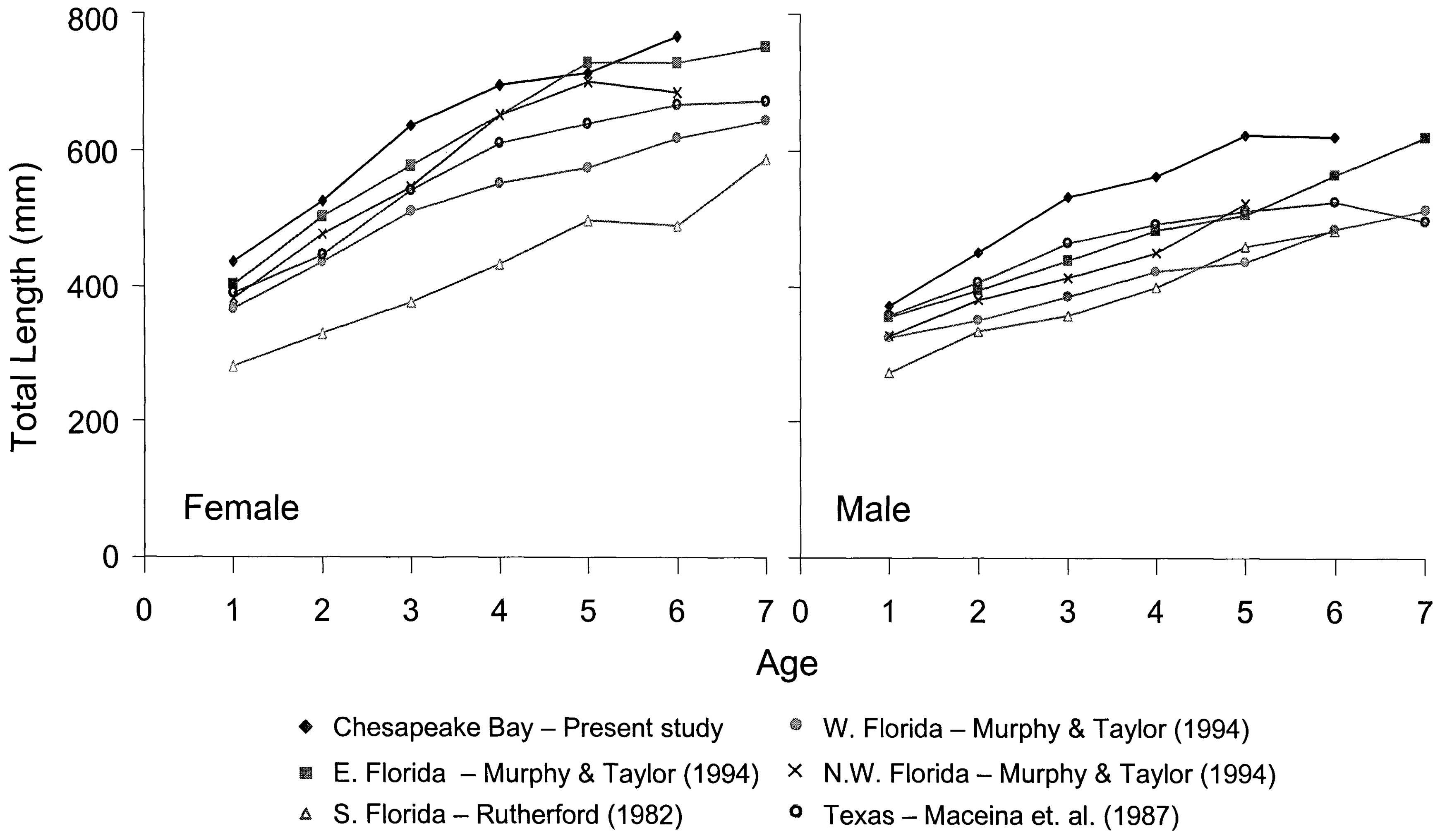


Figure A3. Previously published observed mean size at age for female and male spotted seatrout, compared with the observed mean size at age in the present study.

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